LIFE:
OUTLINES OF
GENERAL BIOLOGY

BY

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PREFACE

Of these large and crowded volumes a brief sketch indicating main endeavours may be of service to the reader at the beginning, and perhaps also at the close; hence a Preface, larger than is customary, may be pardoned.

The aims of this book are broadly fourfold.

(*a*) We give in eight chapters our outline-survey of Biology, in all its essential inquiries into the nature, continuance, and evolution of living beings.

(*b*) We illustrate with more care, and in more detail, than usual, the relations between Biology and the other Sciences—as to Chemistry and Physics on the one hand, to Psychology and Sociology on the other. We have also sought to show how the study of Life, as central among the sciences, and with clear orientation of the sub-sciences of Biology, aids—we even think illumines—the old yet ever-renewing problem of the arrangement of knowledge into an adequate classification of the sciences in general, and this even within their essential fields, their own sub-sciences.

(*c*) Our specific presentment of Biology hence seeks to do justice between "mechanistic" and "vitalistic" doctrines, since we utilise the mechanistic advances, and even formulations, of bio-chemistry and bio-physics for all they are worth, and that is much; yet also show the need of complementing these, by no less due utilisation of psychologic and neo-vitalistic viewpoints and doctrines; and this especially when these are re-stated more concretely, as here in outline we do. For we avoid taking refuge, as older vitalists have done, and some of our contemporaries still do, in metaphysical transcendentalisms, not definitely enough related to the actual processes of Life, in Evolution, and to Life-histories as we naturalists observe them. Central to our thinking are Life's fundamental categories; of Organism, Function, and Environment; and these not merely as separately investigated, but in their varied harmonies, throughout that perpetual interaction which is the essential of Life at all its levels of being and becoming. Hence throughout this book there is reiterated illustration of Organisms functioning in their environments, and of Environments impressing their influences on organisms. And hence, for each and every type of organism, we further seek to appreciate, as far as may be, its Psycho-biosis as well as its Bio-psychosis; in other words, its Mind-body as well as its Body-mind.

(*d*) Besides such expositions and orientations, we submit to the reader various personal contributions, old and new, and outlined a little more fully below—such as our Metabolic Theory of Sex, conception of the Cell-Cycle, arrangement of the diverse types of Animal Behaviour, and fuller analyses of various familiar biological concepts, which have become somewhat conventionalised, such as Reversion, Parasitism, and the Influence of the Environment. Such contributions include, especially in the last quarter of the book, many human and social applications of Biology—medical, eugenic, educational, and even civic.

As to each of these aims, a little more explanation may aid the reader, whether general reader, fellow-worker, or critic from either side.

As to Plan, our book begins with a discussion of the Characteristics of Organisms, which we have grouped in a new chord (Chap. I). We thence begin our comprehensive outline-survey of Biology, starting from the life of organisms as it is lived in Nature; the study of habits and interrelations; in fact the old "Natural History", which is increasingly being developed into the modern sub-science of Ecology (II). A Physiological Section (III, IV, and V) naturally follows, beginning with illustrations of the everyday self-maintaining functions. Hence next an outline of the Species-maintaining functions—a study of Reproduction and Sex. This physiological outline, logically and biologically, leads to the Psychical or Subjective aspects of Life at all levels. Then follows a less detailed introduction to the study of the Structure and Classification of organisms—Morphology and Taxonomy (VI); their individual Development—Embryology (VII); and of their History in the past—Palæontology (VIII). This naturally leads to a necessarily long discussion—yet little more than outline—of the process of Organic Evolution, and of the operative factors, so far as these are known (IX). These nine chapters form the bulk of the book.

The subsequent chapters, of a somewhat different kind, discuss the Position of Biology among the Sciences, and the subdivisions of Biology (X); the Biology of Man (XI); the Wider Aspects of Biology and its applications to the Problems of Human Life (XII); ending up with an outline of a Theory of Life (XIII) here submitted for the first time, save in our little *Biology* in the Home University Series. Three Appendices deal with "Great Events in Biology", "Naturalists at Work", and "The Development of a Biological Outlook". Then comes a Guide to Reading.

The reader will follow our method more clearly by keeping the subdivisions of Biology in view, as graphically outlined on the "End-Papers" of the binding, in their historic treatment—mostly static more than kinetic—so here more vitally arranged:—

BIOLOGY

INTRODUCTORY (I)	ECOLOGY (II)	TAXONOMY (VI)	PALÆONTOLOGY (VII)	PHYLOGENY (IX)	ORIENTATIONS and APPLICATIONS (X–XIII)
	PHYSIOLOGY (III, IV, V)	MORPHOLOGY (V, VI)	EMBRYOLOGY (VIII)	ONTOGENY (IX)	

The roman numerals (in brackets above) indicate the sequence of our chapters. As to proportionate treatment, it will be noted that we have given much more prominence to Ecology than to Taxonomy, much more to Physiology than to Morphology; for this in our judgment expresses the emphasis at present needed to restore the balance of the science, which has been too often and long disturbed by a predominantly post-mortem treatment of organic forms.

While the scope of the book is obviously comprehensive, its treatment is frankly illustrative; so often selecting one topic here and another there, without systematic exhaustiveness, which would have needed a whole series of volumes—themselves but preliminary to the Encyclopædia Biologica of the future, towards which material abounds, yet much more is needed.

Our desire has been to give each chapter not only due inter-relation, but also independent unity enough to be read by itself for the time being, according to the reader's main interest. (This has sometimes involved repetition: thus the story of Proteus is naturally discussed under Environments, yet also under Development; and dimorphism, so extreme in Bonellia, under Sex, and again under Ontogeny. Cross-references are thus reduced.)

In our spacing we have given much attention to such questions as the relation between Biology and the other sciences, and to the mapping out of the field of Biology itself. This is because these questions are usually dealt with in a too perfunctory manner, and because we believe that more thoroughness of treatment will be found of real and practical value, not only for the understanding of Biology, but for orientation of the vast fields of scientific knowledge in general.

In our four final chapters we have freely illustrated some of the many bearings of Biology on a large variety of practically important human problems, from Anthropology onwards. For in our discussion of the relations of Biology to Sociology we have shown the promise there is—as for Medicine and Hygiene, for Eugenics, for Education, for Civics, etc.—in turning from too simply mechanistic theories—as of individual survival, and of economic determinism—to those which come closer to actuality in being more frankly "idealistic", as some may call it—yet after all essentially social.

A little more must be said of the Neo-Vitalism which the general mood and treatment of our book, from its title onwards, endeavours to express. We have illustrated, and emphasised, the indispensable rôles of Bio-Chemistry and Bio-Physics; yet we maintain as firmly that those are still but a finer Chemistry and Physics; hence not fully Physiology, as so many call them, but its preliminary and preparatory studies, and increasingly invaluable as such. Biology proper, with Physiology proper, requires those characteristic concepts of its own, which our first chapter emphasises, and which in our last chapter we further illustrate. Thus the living being enregisters its past, both individual and racial; it exhibits purposive behaviour in its interaction with environment; and with increasing complexity. It grows and multiplies, it develops, it varies, and it evolves, as no mere physical mechanism can do, nor simply chemical process either. While there is a mechanics, chemistry, and physics of the living body, and while these are invaluably progressive alike for thought and in applications, they do not, as a matter of fact, suffice for an adequate description of Life as we know it or live it. Organic life is based on mechanism, but transcends it.

Accordingly we have sought to show—with, we hope, pardonable reiteration—the untenability of a Biology which denies that Mind counts. We have alternated throughout, in presenting the organism,

as far as may be, now as a Body-Mind and again as a Mind-Body. Yet it will be seen that we have given to the advances of bio-chemistry and the physiology of hormones no less space and prominence than to the psychological side of animal behaviour, preferential mating, etc., yet for such latter discussions, and their humanly related ones, the times are surely ripe.

Some main instances of more or less personal contributions, to which we desire consideration from fellow-workers as well as general readers, may be indicated in the successive chapters.

In Chap. I (Characteristics of Organisms) we have given familiar facts a fresh grouping in our re-statement of the criteria of living beings, as compared with non-living systems; and to that we have added what is apt to be lost sight of in conventional definitions—some glimpses of scenes of the Drama of Life in Evolution.

In II (Ecology) one of Darwin's central ideas—the Interrelation of Organisms in the Web of Life—is made the subject of detailed analysis and fresh illustration; and some concepts, as of Parasitism, are radically revised.

In III (Illustrations of Physiology) there is a re-attempted elaboration of certain biological ideas; such as suspended animation in its many graduated forms, the variety of methods in the quest for food, and the relation between the physiological problem of pigments and the ecological problem of coloration; while the concluding section (What is Life?) gives a first broad outline of our neo-vitalist position.

In IV (Reproduction and Sex) will be found a statement of our physiological Theory of Sex, and Sex-dimorphism, first advanced in 1889, and now supported by much additional evidence. As indicated in our previous smaller books—*Sex*, *Biology*, and *Evolution*, these conceptions have wider bearings, and applications, than are yet generally recognised.

In V (Bio-Psychological) there is an attempt to arrange in an evolutionary gradation all the many modes of Animal Behaviour, and an (eirenic) attempt to intermediate between the extreme Behaviorists on the one hand and the extreme Anthropomorphists on the other.

In VI (Morphological) there is a fresh outline-statement of our (long-maintained but as yet seldom considered) Concept of the Cell-Cycle, which seems to us a vital idea in Cytology, as also in Evolution. Here also an attempt is made to re-analyse certain familiar ideas in morphology, such, for instance, as those of "Rudimentary" and "Vestigial" Organs.

In VII (Development of Organisms) we have given prominence to a rehabilitation of a very old idea—that of "the Curve of Life". This trajectory—with its various phases—is illustrated, less or more vividly, by all typical life-histories, of plants and animals alike; and we have shown how a lengthening-out or a shortening-down of various arcs of the curve aids in accounting for many of the differences in and between related species, and even types.

In VIII (Great Steps in Organic Evolution) we have faced the problem of the major advances in structure and function, so often left obscure in the evolutionary succession of races of organisms;

and we have insisted on the value of seeking to correlate these organismal advances with the changes in the world-environment. Here again, as also in XII, there is emphasis on the idea of the Cell-Cycle. Perhaps we may also refer to a fresh note struck in our brief discussion of the old questions of the possibility of life beyond our terrestrial limits.

In IX (Factors in Evolution) we have made not a few suggestions:—such as (*a*) the interpretation of evolutionary Variations, from small to greater, in terms of alternatives in the ratio between anabolism and katabolism; (*b*) the exposition of physiological trends of Variation in Plants, with particular reference to the relation between nutrition and reproduction (a conception also applicable as regards the evolution of animals); (*c*) the definition and illustration of the rôle of "Nurture" in individual development, and in racial evolution; (*d*) the analysis of reversionary phenomena, carried further than usual; (*e*) the further working out of the Darwinian idea of the Web of Life as of selective value; and (*f*) the clearing up of ideas and terminology throughout the main sciences, in the section on "Different Kinds of Evolution".

We need not continue our instances of more or less personal contributions in the later chapters of the book (X–XIII) and its three appendices, though it is perhaps here that they are most numerous, and sometimes most adventurous; since even to intrusion upon the current discussion of the Relativity-doctrine; and to the suggested projection of the technique of our treatment of Life towards the presentment of main ideas of the physical sciences. This indeed some of their recent thinkers, as notably Whitehead, are already beginning to do.

A final personal word. While the writers have been collaborating with substantial agreement since (and even before) their *Evolution of Sex* (1889), their work and thought have mostly been in very different and distinct fields; whence naturally much discussion as to the scope, perspective, and co-adjustment of their respective studies of Life, and in its Evolution. Thus while every chapter, section, and even paragraph has been mutually criticised, and so far adjusted, certain shades of difference remain, as especially of outlooks, respectively more of Neo-Darwinian and Neo-Lamarckian tendencies. Still, our book has also gained something towards its treatment of problems still far from complete solution, from experiences in Nature so largely different yet mainly complemental; and from lives so long and often separate, yet with renewing co-operations in comradeship.

We must thank our old artist-friend, Mr. William Smith, for his careful skill in making the illustrations, many from actual specimens; and also various authors and publishers for certain figures. Thus, too, Messrs. Thornton Butterworth, Ltd., for re-drawing of our End-Papers from diagrams in our *Biology* in their Home University Library. Finally, we thank our publishers for their considerate patience with the authors' delays over their long and ambitious endeavour.

J. A. T.
P. G.

EXPLANATION OF "BIOLOGY IN SUB-SCIENCES" END-PAPER

Graphic Outline of BIOLOGY, in its eight SUB-SCIENCES, respectively Analytic and Synthetic, i.e. of Individuals and Groups :—

From observation in Static Aspects, as FORMS, Present or Past	*ANATOMY (including Histology), e.g. Bird's Skeleton.* *TAXONOMY (classification), e.g. Bird-Types in Museum.*
MORPHOLOGICAL SUB-SCIENCES	*EMBRYOGRAPHY, e.g. Phases in Frog's development.* *PALÆONTOGRAPHY, e.g. Fossil (Trilobite).*
From observation to interpretation in Kinetic Aspects, FUNCTIONINGS, Present or Possible	*PHYSIOLOGY, e.g. Plant growing in Environment. Note two Life-Function-Systems—self-maintaining (Nutritive), and species-maintaining (Reproductive)—each with sub-functions.* *ECOLOGY, e.g. Web of life: Interrelations.*
PHYSIOLOGICAL SUB-SCIENCES	*ONTOGENY: Larva—Pupa—Imago: Functional Interpretation.* *PHYLOGENY: Plant as symbol towards genealogical tree: in branching, leafing, flowering, etc.: Functional Interpretation.*

EXPLANATION OF "SCIENCES IN GENERAL" END-PAPER

(A)—Lowest on the left, the field of pure Mathematics, is marked by axes in three dimensions.

The space or step above this, towards the right, indicates the field of the Physical Sciences, symbolised by the Balance.

In the next space (above to right) the field of Biology, indicated by the Scarabæus.

And in the last space (above to right) the field of Sociology—indicated by the Book; and marked "T" and "S" for its "Temporal and Spiritual" elements, more or less conspicuous in each and every form of Social Life, and in its Heritage (and Burden).

(B)—Descending in reverse order, note, behind the Book, for Sociology, Moses' Tables of Commandments, as old symbol for Ethics. Beyond the Scarab of Biology spreads the Butterfly (Psyche) *of Psychology. Above the Balance for Physical Science, the Rainbow* (Iris) *of Esthetics: and around the Mathematical Axes the swirl of Logic, as most universal of all sciences. This descending series of subjective sciences is in Plato's order; of "Good, True, and Beautiful"; and is thus complemental to the previous ascending series—that from Aristotle to Bacon, Comte to Spencer, and modern scientific workers generally.*

(C)—Again in ascending order, note that each main science, shown on its step, is preliminary to the succeeding one—and also extends on its own level below it. Thus Mathematics primarily subserves the Physical Sciences; yet also Biology, as Biometrics; and Social Science, as Statistics. The Physical Sciences similarly underlie Biology (as Bio-Mechanics, Bio-Physics, and Bio-Chemistry); and even the Social Sciences also, since all in physical environments. Biology underlies Social Science; since the Social life of Region and State, City and Citizen, are all biologically conditioned (as by Physiology and Hygiene, with Heredity, Eugenics, etc.).

Yet each succeeding science retains its own distinctiveness—as fresh "Emergence". Hence with the clear foundation of Sociology, on "the preliminary sciences", their respective underlying contributions were defined as so many "legitimate Materialisms". *Only when the needed preliminary contribution—to each main field or fields above—is mistakenly assumed sufficient to supersede it or them (as too often by their most active cultivators, and thus their readers) do "illegitimate Materialisms" arise. Bio-Physicists and Bio-Chemists for Biology, and Hygienists and Eugenists for Sociology, are alike often liable to such errors.*

(D)—The interrogation-marks in the six spaces otherwise vacant (to the left of the diagonally ascending stair of the main sciences) indicate the fields for inquiry into the suggestive contributions of each higher science to its so far "preliminary sciences". Hence then for the evocations from Social Life and Science to Biology and Psychology. Biology has similarly aided Physical Science; and Psychology Esthetics; and similarly Physical problems evoke Mathematical methods, and even advance Logic.

Such inquiries (see Appendix II) have been termed "legitimate transcendentalisms"—and are to be distinguished from "illegitimate" ones;—as of some philosophers, with inadequate knowledge of the sciences, and sometimes by their specialists as well. Thus each and every one of the sixteen fields of this Graphic needs and rewards full investigation, alike for its own sake, and for its services to others. The Unity of Science has thus to be realised.

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INTRODUCTORY

WHAT IS BIOLOGY?

WHILE everyone recognises that Biology is Life-science, this is but a translation, not a definition. In its original and best usage, Biology means an inquiry into the nature, continuance, and evolution of living creatures. It does not, indeed, seek to describe all kinds of organisms, for that is the task of its main sub-sciences—Botany and Zoology, with Protistology and Bacteriology; and many claim Anthropology as well; it deals rather with the problems and generalisations that are common to all living creatures, and on which each line of specialism throws its particular light.

In a classification of the sciences it is convenient to use the term Biology to include all the biological sciences, as contrasted with chemistry and physics on the one hand, psychology and sociology on the other; but the stricter usage—which began, about 1801, with Treviranus and Lamarck, by whom the word was independently proposed—keeps the term for the study of the general questions that apply to all forms and processes of organisms. What is the nature of that particular kind of activity that we call "Life"; how does the individual organism begin and develop; how does it persist from day to day and continue its kind, sometimes in slightly changed expression, from generation to generation? It is in this sense that the word Biology is used in this book.

A third and indefensible usage, common in Germany, is as an equivalent for Ecology, or the study of habits and inter-relations. Sometimes, however, it is convenient to speak of "The Biology of Birds", or "The Biology of Insects", or the like, to denote a book or treatise that deals with a particular class or type in such a way as to illustrate and contribute to General Biology.

A scientifically inquisitive mind—such as we hope our reader's is—is often inclined to begin a biological inquiry with the question: *What is Life?* But this is obviously not a beginner's question; it is more likely to be answered, and then but tentatively, towards the end of our studies. So in this book let us begin not with "Life", but with a concrete and descriptive study of the characteristics of *living organisms*, and with glimpses of the life-drama in which they play their part. The first step is to fill the mind with vivid impressions of organisms as active agencies, prompted by hunger and love and the will to live, seeking more life in their developing, growing, and multiplying, and rarely ceasing to be insurgent against environing difficulties and limitations. Life may be traced down into par-

ticular—yet many-sided and even protean—activity in colloidal protoplasm; but it is more profitable to lay the first emphasis on the everyday activities of the organism as a whole. Hence the second part of this Introduction deals in a broad way with the characteristics of living creatures—Lives in being.

ECOLOGICAL.—Here our initial question changes its form; and we are led to inquire into the ways of living creatures as they live in Nature. In the mood of the old-fashioned Natural History, but with the precision which renews this as Ecology, we here study organisms in relation to their environments, and in the seasonal and other changes of these. This discloses a web of inter-relations, a vibrant Systema Naturæ—say, rather, Drama Naturæ—in which nothing lives or dies to itself. For there is a fascinating variety in the nutritive chains which bind living creatures together in a series of successive re-incarnations or re-embodiments; there are helpful partnerships like commensalism and symbiosis, yet there is also predatory life, and the competition it so especially provokes; yet also there are evasions of the competitive struggle for existence, as in the sheltered nooks of life, or in parasitism. Thus the part of this book that is headed ecological is naturally long as well as varied. This mode of approach is, we submit, psychologically natural, and it corresponds with the historical development of biological science.

PHYSIOLOGICAL.—But equally essential and irrepressible is the physiological question: How does this organism work? How does it keep going? How does it feel and move? How does it grow and multiply? How does it waste, yet recover itself? And finally, in all but the simplest, how does it die? Here we brush aside the old answers which speak of "vital spirits" and "vital force", of "principles of life", and so on, yet not forgetting that we may sometime rehabilitate the truth in such too abstract expressions. More resolutely than in old days, we have to analyse the workings of the different organs which co-operate in the life of the whole, such as the throbbing heart and the churning digestive stomach; we pass beneath this to study the tissues that build up the organs: the contracting muscles, the thrilling nerves, the secreting glands; we inquire yet more penetratingly into the waxing and waning of the component cells; and at length we reach the complex chemical and physical changes that go on in the protoplasm. And as the intricacy of these internal activities impresses the student, the question naturally arises how they are all integrated—as it were orchestrated—so that the result is efficiency of action and the harmonious vigour of positive health. The answer to this question leads beyond the integrative functions of nervous and circulatory systems to the modern discovery of the regulative rôle of "hor-

mones". This analysis of self-maintaining activity has to be applied, of course, to plants as well as to animals, hence the long discussion of Plant Physiology.

But the marvellous efficiency of the organism's self-maintaining and self-repairing has its counterpart in its power of giving rise to other organisms in its own likeness. This line of functioning stands in some ways by itself, and, though its apartness has been overemphasised in the past, it is practically necessary to devote several chapters of this book to the physiology of Reproduction and Sex. For all this has to be traced upwards from the simple divisions and unions of unicellular organisms, and thence onwards to the often strange and intricate life-secrets of higher forms, and at length to their uttermost veiling—yet now unveiling—within the apparently simple flower, conspicuous though, as in the lily, its sexes long seemed. On the animal ascent we come to the elaborate courtships of many birds, the various conjugal ways of mammals, and the parental relations in both. For the relations between the two sexes cannot be adequately understood apart from parental functioning, and often care.

BIO-PSYCHOLOGICAL.—In discussing many physiological questions, and ecological ones yet more, as from the working of the nervous system to the migration of birds, it becomes impossible to ignore the psychical aspect; and this is surely increasingly prominent in mating and in mothering. Thus we are naturally led to a bio-psychological inquiry, for the animal kingdom at least,—an arrangement of the different levels of behaviour, from simple reactions to reflexes, from obligatory movements to instincts, from the simple "trial and error" of a food-testing spider to the surely intelligent grasp of a situation by a sheep-dog or by a chimpanzee. Here must be faced the perennial "mind and body" problem, and even that of the not impossible rôle of mind as a factor in evolution. Such are some of the difficult tasks for the section called bio-psychological.

MORPHOLOGICAL.—Side by side with the question, How does this organism or organ work? there has developed the question, What form and structure has this in itself, and in all its parts? This seems a simple question, but how difficult to answer, as we press it further and further home, from external features and symmetry to internal structure, from organs to tissues, from these to cells and the living matter that composes them. How intricate the answer must become as the structural analysis deepens, as we put one lens after another in front of our own, as we call to our aid all sorts of devices—from scalpel and forceps, to begin with, to razor and microtome, fixative and stain. Dissection, even of minute animals, has been carried to a high perfection by a long succession of zoo-

logical anatomists of surpassing skill, as from Réaumur and Lyonet to Lacaze-Duthiers and Delage. But the acheivements of hand-controlled dissecting needles are now far surpassed by the microscopic manipulations which enable Robert Chambers, and his students too, to excise the nucleus from an amœba, and even dissect it! This inquiry into the static aspect of organisms—their structure in general and in detail—leads to a recognition of their characteristic architectural plans and styles, and even discloses their engineering principles of construction. Moreover, it leads us to perceive, through comparative anatomy, certain deep-seated structural resemblances or "homologies" by help of which our old popular and "Natural History" classifications—e.g. of all sorts of marine creatures as "fish"—have long been in process of replacement by more rationally architectural ones. Thus comparative morphology affords the basis for classification proper, commonly called Taxonomy. This, in fact, is the subject of Linnæus's fundamental Opus —his *Systema Naturæ*—from the tenth edition of which (1758) systematic botanists and zoologists have long been agreed to date the opening of their era. For though the Drama Naturæ, scene by scene, has its spectator and recorder in the ecologist, it is the service of the taxonomist to enumerate and arrange the Dramatis Personæ, as for the comparative anatomist to supervise it. Hence an important though brief section of this book deals with the principles and results of the inquiries into organic architecture and orderly arrangement.

DEVELOPMENTAL.—The study of adult structure, from Aristotle to the anatomist of to-day, naturally leads to inquiry into earlier stages; and thence back to the embryo and to the egg. Thus arose the description of the individual Becoming or genesis: descriptions of the developing chick within its shell, the bee-grub in its waxen chamber, the embryo skate within the "mermaid's purse", and the tadpole forming within its sphere of spawn-jelly. How arises the individual organism—plant as well as animal, as a whole and in each of its parts? The answer to this question—to which a corresponding physiological one has to be added—is Embryology.

But this developmental question cannot be restricted to eggs and embryos; it must be extended to larval and adolescent stages; it must be continued throughout the whole biography up to adult form and life. There even arises a still wider conception of this sub-science, as including not only progressive changes, but retrogressive as well. These retrogressions or involutions may begin very early, and also reappear with age, in the waning of strength in normal senescence, and, in a few cases among animals, but often in mankind, beyond this into disintegrative senility. Hence the life of the

developing individual must be thought of as on a curve—a trajectory—with its ascent and its descent alike, often with characteristic "ages" or phases. And again, we must think of each of these phases as having its possibilities of lengthening or shortening in adaptation to particular habits and conditions. All this is discussed in the section of the book that deals with the Development of Organisms.

PALÆONTOLOGICAL.—But the inquiring student, who has grasped for the individual organism the idea of Becoming, cannot but look for its counterpart in the story of each race; in fact, just as we study a Biography in its place in History. The horse was once a foal, and the foal was once a fœtus in the womb of its mother; and the story of this is *embryological*; but the race of horses has had its long-drawn-out evolution, from the small four-toed and three-toed Eohippus of the Eocene meadows to the stately modern Equus running and leaping on the tiptoe of one digit on each limb; and the story of this is Palæontological.

In other words, embryology has to do with individual development (ontogeny), and palæontology has to do with racial evolution (phylogeny). But the two must be correlated, even at the risk of a vicious circle, for the palæontologist, whose main material consists of fossils, may receive hints from the embryologist, who has sometimes been the first to discern relationships; and the embryologist may get light from the palæontologist, since the individual development tends to be in some respects an abbreviated recapitulation of the racial evolution.

Palæontology describes, as far as possible, the gradations that may lead, among fossils, from one species to another (particularly well illustrated in Planorbis and other fresh-water snails); the connecting links between distinct types (well seen in extinct Cephalopods), the affiliation of classes (as of Birds from Dinosaurian Reptiles), and even the origin of a particular association of organisms, such as the Deep Sea Fauna or the Carboniferous Forest. Thus there may be a palæontology of species, types, classes, phyla, and associations. With the last may be included an inquiry into geographical distribution, how different countries have come to be tenanted by similar or dissimilar faunas and floras. In essence, palæontology is a description of the stages by which organisms have come to be as they are; and it fails of its ambition if it does not disclose something of the grandeur of the historical Ascent of Life. It is this most general aspect of Palæontology that is emphasised in the outline which this book offers; hence the title of the palæontological section—*Great Steps in Organic Evolution*.

ETIOLOGICAL.—Huxley applied the useful term Etiology to the study of the factors that have operated in the process of

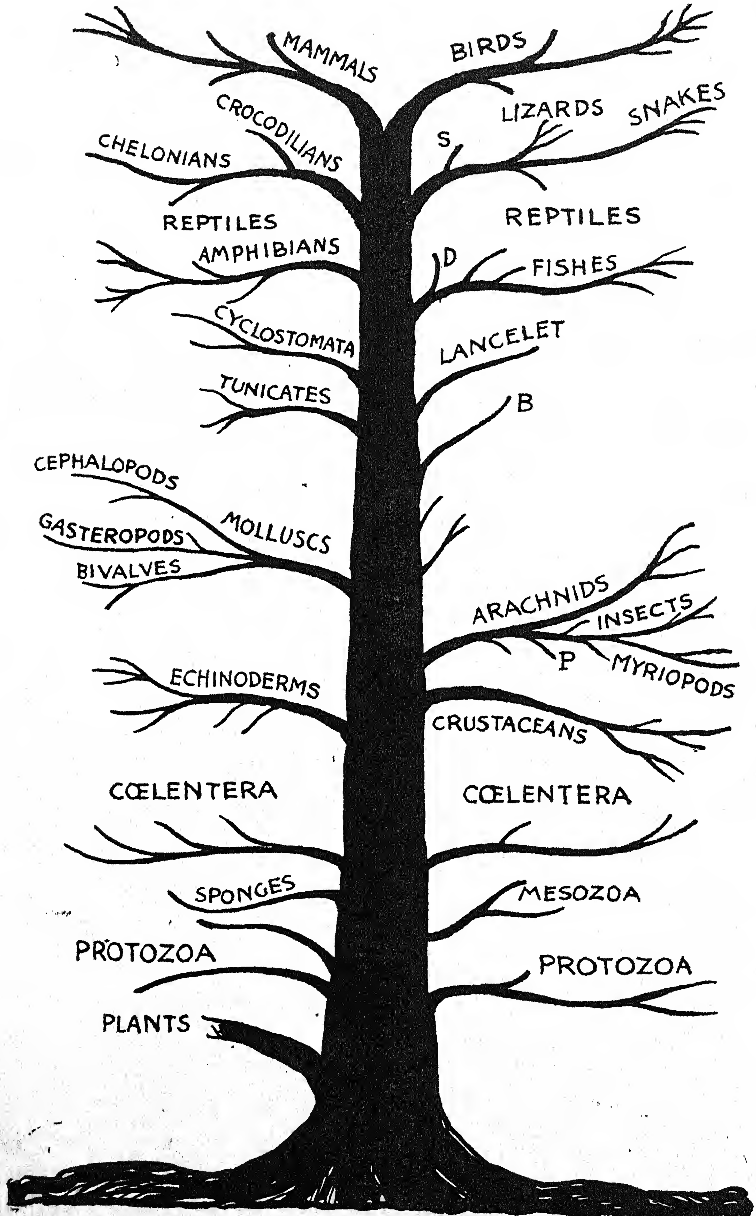


FIG. 1.

Tentative Genealogical Tree of Animals. P, Peripatus; B, Balanoglossus; D, Dipnoi or Lung-fishes; S, Sphenodon or New Zealand "Lizard".

Organic Evolution. It is one thing to state that Birds evolved from an extinct stock of Reptiles; it is another thing to try to indicate, by analogy from the present day, what factors were at work in this notable emergence which took place millions of years ago. Etiology is an inquiry into the causes of phylogeny, or the origin of races, but it must be based on the observational and experimental study of present-day variation and heredity, selection and isolation. Account must be taken of the plasticity of living creatures in the hands of their environment, of the shufflings of the hereditary cards during the maturation and fertilisation of the germ-cells, and also of the factors that come into play in the early stages of development. Here have to be discussed the particular theories of evolution that are associated with Lamarck, Darwin, Weismann, and their successors. Thus a large section of the book is entitled Evolution-Theory; for that is what Etiology comes to.

So far, then, a logical plan: Ecology and Physiology, Taxonomy and Morphology, Embryology and Palæontology, and then all the problems of Etiology. It will be understood, of course, that these logical sections are not to be regarded as pigeon-holes with rigid walls; for the organism is a unity whose various aspects cannot be separated off except for purposes of convenience. Thus the consideration of a function necessarily raises the question of the structural arrangements by which it is carried out; and the anatomical analysis of an organ necessarily raises the question of the utility of the several parts. Similarly, the evolution-question: "By what steps and by what factors did this come to be as it is?" must be behind or beneath all the other inquiries, whether anatomical or physiological, whether dealing with embryos or with fossils.

Our book contains tentative answers to four great questions. Of these the first asks how Biology stands among the other sciences, how it is related to Chemistry and Physics below it, and to Psychology and Sociology above it. What is the most convenient grouping of the sciences, and how are they distinguished in their methods and categories? Here, more profitably than at the outset, the question: *What is Life?* has to be considered; and the long-standing controversy between the mechanists and the vitalists, whose descriptions are complementary rather than antithetic.

Then comes the question of Man's place in Nature, his apartness from the animal kingdom, and yet his solidarity with it; his vaguely discerned pedigree, and the factors in his ascent. This leads on to an indication of the biological contributions to Sociology.

From this it is natural to pass to the applications of Biology to the furtherance of Man's welfare. How has Biology contributed to the progress of Agriculture and Fisheries, Medicine and Hygiene? And how far are biological methods and results of value in regard

to the practical problems of social life, in reference pre-eminently to education and eugenics?

The last question concerns the science itself. What in outline is the history of Biology, what have been the great steps in its advance, and who have been its most significant makers? This naturally leads to a selected bibliography, which aims only at being representative.

LIFE: OUTLINES OF GENERAL BIOLOGY

CHAPTER I

THE CHARACTERISTICS OF ORGANISMS

FROM a common-sense point of view the apartness of living creatures from non-living things seems conspicuous. It appears almost self-evident that an organism is something more than a mechanism. But when we inquire into the basis of this common conviction, we usually find that the plain man is thinking of the highest animals, such as horses and dogs, in which he recognises incipient personalities, in a world quite different, he says, from that of machines, or from that of the stars or stones. His conviction rests on his recognition of them as kindred in spirit; but he hesitates when we ask him to consider the lower animals, down to corals and sponges, and still more when we ask what he thinks about plants. In such relatively simple organisms as corals and seaweeds, he detects no mental aspect; and apart from this, they show him but little of that bustling activity which is part of his picture of what "being alive" means. Thus, while he was sure that dog and wheelbarrow were separated by a great gulf, he is not so convinced about the difference between a coral and a stone. It is, therefore, for the biologist to explain as clearly as he can the fundamental characteristics of all living creatures. And there is another reason for this.

One of the earliest imaginative ventures of primitive man was to project *intention* into outside forces and non-living things. Having little understanding of the physical world, and almost as little mastery of it, he projected himself into forces and things. In the absence of more than the beginnings of scientific description, primitive man had somehow or other to make sense of things; so he pictured them as agents like himself—a view that expanded later on into a general theory of animism, peopling the world with spirits: in fact a *volitional* view, derived from his own conscious will.

Now the question which we must frankly face, in seeking to distinguish the characteristics of living organisms, is whether we biologists, in our turn, doubtless a higher one, are not in danger of repeating the mistakes of our ancestors. Our scientific knowledge of the organism is very incomplete; we do not know all that living may essentially mean; we feel sure that we do not exhaust it even

when we add to all we know of vital processes the available contributions of chemistry and physics; and thus biologists have tended, if not to shirk analysis by spelling Life with a capital, at any rate to be too easily satisfied with regarding the living creature now as an historically developed being, or again as a psycho-physical individuality. Yet such interpretations are regarded by the extreme bio-mechanists as no better than any other anthropomorphic notions. This is another reason, then, for a careful consideration of the characteristics of the organism.

PERSISTENCE IN SPITE OF CEASELESS CHANGE.—The symbol of the organism is the burning bush of old; it is all afire, but it is not consumed; *nec tamen consumebatur*. The peculiarity is not that the organism is in continual flux, for chemical change is the rule of the world; the characteristic feature is that the changes in the organism are so regulated that the integrity of the system is sustained for a longer or shorter period. That excellent physiologist, Sir Michael Foster, used to say that "a living body is a vortex of chemical and molecular change"; and the image of a vortex expresses the fundamental fact of persistence, in spite of continual flux.

Here it is fitting to quote one of the classic passages in modern biological literature, what Huxley said of the vital vortex in his *Crayfish* (1880, p. 84):

"The parallel between a whirlpool in a stream and a living being, which has often been drawn, is as just as it is striking. The whirlpool is permanent, but the particles of water which constitute it are incessantly changing. Those which enter it, on the one side, are whirled around and temporarily constitute a part of its individuality; and as they leave it on the other side, their places are made good by new-comers.

"Those who have seen the wonderful whirlpool, three miles below the Falls of Niagara, will not have forgotten the heaped-up wave which tumbles and tosses, a very embodiment of restless energy, where the swift stream hurrying from the Falls is compelled to make a sudden turn towards Lake Ontario. However changeful is the contour of this crest, this wave has been visible, approximately in the same place, and with the same general form, for centuries past. Seen from a mile off, it would appear to be a stationary hillock of water. Viewed closely, it is a typical expression of the conflicting impulses generated by a swift rush of material particles.

"Now, with all our appliances, we cannot get within a good many miles, so to speak, of the crayfish. If we could, we should see that it was nothing but the constant form of a similar turmoil of material molecules which are constantly flowing into the animal on the one side, and streaming out on the other."

The comparison has great force and utility; it vivifies the funda-

mental fact that streams of matter and energy, such as food and light, are continually passing into the organism, and that other streams are continually passing out, for instance in the form of carbon dioxide and heat. On the other hand, the comparison has its weakness and possible fallaciousness; for it is too simple. It does not do justice to the characteristic way in which the organism-whirlpool acts on the stream which is its environment; it does not do justice to the characteristic way in which the organism-whirlpool gives rise to others like itself. No one who believes that higher animals (at least) have a mental aspect that counts, can agree that the organism is exhaustively described as "nothing but the constant form of a turmoil of material molecules." And even if the mental aspect be ignored, there remains as a fundamental characteristic that the "constant form" is secured by organic regulation from within. Life is nothing if not *regulative*.

Biology has come nearer the crayfish since Huxley's day, and it is profitable to linger over the fact that the living creature persists in spite of its ceaseless change. As a matter of fact it persists because of the self-repairing nature of its ceaseless change. Hence we give prominence to this material flux.

METABOLISM OF PROTEINS.—Proteins are nitrogenous carbon-compounds that are present in all organisms, and, apart from water, of which there is seldom less than 70 per cent., they constitute the chief mass of the living substance. They are intricate compounds, with large molecules, which are built up of groups of amino-acids, i.e. fatty acids in which one of the hydrogen atoms is replaced by the *amino*-group NH_2. Proteins, such as white of egg, or the casein of cheese, or the gluten of wheat, do not readily diffuse through membranes; they occur, as will be afterwards explained, in a colloid state, and although some, e.g. hæmoglobin, the red pigment of the blood, are crystallisable, they are not known in a crystalloid state in the living body. Though relatively stable bodies, proteins are continually breaking down and being built up again within the cells of the body, partly under the direct influence of ferments or enzymes.

There are constructive, synthetic, upbuilding, or winding-up chemical processes always going on in the living organism, which are conveniently summed up in the word *anabolism*, applicable, of course, to the synthesis of other carbon-compounds besides proteins, notably to the formation of carbohydrates in the sunned green leaf. There are also disruptive, analytic, down-breaking, running-down chemical processes always going on in the living organism, which are conveniently summed up in the word *katabolism*—applicable, of course, to other carbon-compounds besides proteins, as, for example, to the breaking down of amino-acids into

fatty acids and ammonia. To include the two sets of processes, anabolism and katabolism, the general term metabolism is used. It is convenient to use this term in a broad way, as the equivalent of the German word "Stoffwechsel" (change of stuff), to include all the chemical routine of the living body. The present point is that living always involves the metabolism of proteins; and that this is so regulated that the living creature lives on from day to day, or from year to year, even from century to century.

There is intense activity of a simple kind when the fragment of potassium rushes about on the surface of the basin of water, but it differs markedly from the activity of the Whirligig Beetle (Gyrinus) that swims swiftly to and fro, up and down in the pool. The difference is not merely that the chemical reactions in the beetle are much more intricate than is the case with the potassium, and that they involve eventually the down-breaking and up-building of protein molecules. The big difference is that the potassium fragment soon flares all its activity away and changes into something else, whereas the beetle retains its integrity and lasts. It may be said, indeed, that it is only a difference in time, for the beetle eventually dies. But this is to miss the point. The peculiarity we are emphasising is that for certain variable periods the processes of winding-up in organisms more than compensate for the processes of running down. A primitive living creature was not worthy of the name until it could balance its accounts for some little time, until it could in some measure counter its katabolism by its anabolism. Perhaps it was only a creature of a day, which died in the chill of its first night, probably after reproducing its kind; but the point is that during its short life it was not like a glorified potassium fragment or a clock running down. It was to some extent winding itself up as well as letting itself run down. It was making ends meet physiologically.

In the immense furnaces of the stars, with unthinkably high temperatures, it may be that hydrogen is being lifted up into more complex forms of matter, but on the earth all the chemico-physical clocks are running down. Uranium, by a partial disintegration of its atomic nucleus, may give rise to ionium, which may give rise to radium, which by giving off helium may give rise to lead. Or uranium may give rise to protactinium, which produces actinium, which produces lead. Other instances are well known. But while lead seems to be readily born and does not die, there does not seem to be at present on the earth any process working the other way and producing heavy atoms like those of uranium. In the little corner of the universe where we move, we are living in a time of the running down of chemico-physical clocks. But the characteristic of living organisms is that they wind themselves up.

In an essay entitled *The Abundance of Life*, published many

years ago (1891), republished in *The Birth-Time of the World* (1915), Prof. Joly laid emphasis on the organism's power of accumulating energy. The more heat energy is put into an iron bar, the more difficult it becomes to get in more, and the more readily does some of the heat radiate out. But it is different with the living creature; it absorbs energy acceleratively and accumulatively. Prof. Joly puts the case tersely:

"The transfer of energy into any inanimate material system is attended by effects retardative to the transfer and conducive to dissipation. The transfer of energy into any animate system is attended by effects conducive to the transfer, and retardative of dissipation. . . . The animate system is aggressive on the energy available to it, spends it with economy, and invests it with interest, till death finally deprives it of all."

Colloidal Protoplasm.—The accumulation of energy in organisms is mainly effected by storing complex chemical substances, not merely as reserves in the ordinary sense, like the plant's starch and the animal's fat, but in the living substance itself in the form of increased protein material. The chemical formula of egg-albumin, to take a familiar protein, is often given as $C_{1428}H_{2244}N_{364}O_{462}S_{14}$; and this hints at the complexity of these substances. In the strict sense, protein material does not form definite stores in animals, though it is a common reserve in the seeds of plants, but it accumulates as the amount of living matter increases. The potential chemical energy of the complex carbon-compounds found in living cells is particularly valuable because the living matter occurs in a colloidal state. Of this it is enough in the meantime to say that a watery "solution" holds in suspension innumerable complex particles, too small to be seen, even with the microscope, but large enough to have an appreciable surface. The particles do not clump together or sink because each carries an electric charge, and like charges repel one another. Even a metal like gold can be readily made to assume this colloidal form. In some colloids, however, as may be illustrated by liquid gelatine, the particles are, as it were, protected by a coat of water molecules, and such particles are spoken of as "emulsoid", in contrast to "suspensoid", as in the case of liquid gold. But everyone knows that the cooled gelatine sets, the "sol" becoming a "gel". In this state the particles adhere to one another and give some rigidity to the whole. The alternation of "sol" and "gel" plays, as we shall see, an important part in vital processes. Proteins always present themselves in the colloidal state in living organisms, and it is clear that they thus afford, in their innumerable particles, a large surface on which chemical and physical changes can take place.

Specificity.—Each kind of organism has its chemical individuality, implying a specific molecular structure in some of the

important constituents, and a corresponding routine of reactions. This is particularly true of the proteins, and there are probably special proteins for each genus at least. There is chemical specificity in the milk of nearly related mammals, such as sheep and goat; and, as Gautier showed in detail, in the grape-juices of nearly related vines. A stain due to the blood of a rabbit can be readily distinguished from a stain due to the blood of a fowl or of a man. More than that, as Reichert and Brown have demonstrated conclusively (1909), the blood of a horse can be distinguished from that of an ass. The crystals of the hæmoglobin or red blood pigment of a dog differ from those of a wolf, from which the dog evolved, and even from those of the Australian dingo, which seems to be the result of domesticated dogs going wild and feral. Even the sexes may be distinguished by their blood, and there are two or three cases among insects where the colour of the male's blood is different from the female's. The familiar fact that some men cannot eat particular kinds of food, such as eggs, without more or less serious symptoms, is a vivid illustration of specificity. It looks as if a man was individual not merely in his finger-prints, but as to his chemical molecules. Every man is his own laboratory. Modern investigation brings us back to the old saying: "All flesh is not the same flesh: but there is one kind of flesh of men, another flesh of beasts, another of fishes and another of birds."

We shall return to specificity in discussing species, but we must emphasise the fundamental fact that the different kinds of animals and plants are very like the chemical elements in their individuality. Each is itself and no other. Perhaps the change from one organic type to another, a brusque change which we call a large mutation, is comparable to the change from uranium to lead. Perhaps the change from one variety to another, which we call a fluctuation or minor variation, is comparable to the change from one ethyl-compound to another.

To some who have not looked into the matter it may seem almost preposterous to speak of a particular protein for every genus at least. But the work of Emil Fischer and others has shown that there is inconceivable variety in the groupings and proportional representations of the twenty-odd amino-acids and diamino-acids which constitute in varied linkages the complex protein molecules. There must be a million million possibilities and more. As there are about 25,000 named and known species of Vertebrates and about 250,000 (some would say 500,000) named and known species of Invertebrates, there may readily be particular proteins for every species of animal, leaving plenty to spare for all the plants.

GROWTH, MULTIPLICATION, AND DEVELOPMENT.—The organism's power of absorbing energy acceleratively, and of accu-

mulating it beyond its immediate needs, suggests another triad of qualities—growing, reproducing, and developing, which may be profitably considered together. As Prof. Joly says in the essay already referred to: "The organism is a configuration of matter which absorbs energy acceleratively, without limit, when unconstrained . . ." The young leaf spread out in the sunlight utilises a fraction of the solar energy that pours upon it, and does so acceleratively; the more it gets, the more it grows, and the more it can take. This is the unifying idea behind the familiar, though still mysterious, powers of growing, multiplying, developing, and growing again.

GROWTH.—The power of growth must be taken as a fundamental characteristic of organisms, for it cannot as yet be re-described in chemical and physical terms. The word is a convenient label for a variety of processes which lead to an increase in the amount of living matter, and while there are chemical and physical factors involved in these processes, we are bound in the present state of science to admit that growth depends on the veiled tactics of life. Its results are extraordinary achievements, which would be astounding if they were not so familiar. From a microscopic egg-cell there develops an embryo-plant which may grow, say, into a Californian "Big Tree"—perhaps three hundred feet in height and over three thousand years old. A frog is about three or four inches in length, its egg-cell is under a tenth of an inch in diameter; "the mass of the human adult is fifteen billion times that of the human ovum." In the strict sense growth means an increase in the amount of the organism's living matter or protoplasm, but it is often associated, as in a cucumber, with great accumulation of water; or, as in the case of bone, with the formation of much in the way of non-living walls around the living cells. Growth is usually effected by the multiplication of cells, but in some cases, especially in certain plants, there is first an increase in the mass of living matter, and secondarily a segregation of portions of this into distinct cells—a partitioning that makes it easier for the intricate bustle of life to continue without disorder. When a nerve-fibre grows on and on, feeling its way, as it were, into the distant parts of the growing body, there is growth without cell-division; and the same is sometimes seen, even in an adult, when a muscle-cell grows greatly in length and breadth.

The indispensable condition of growth is that income be greater than expenditure. A variable amount of the food-income is used to meet the everyday expenses of living; the surplus is available for growth; and this must be understood as including, besides increase in size, that imperceptible growth which brings about the replacement of worn-out cells by fresh ones. Green plants are great growers when compared with animals—the Giant Bamboo may

grow a foot in a day—and that is mainly because they get food-materials at a low chemical level, that is to say from the air and

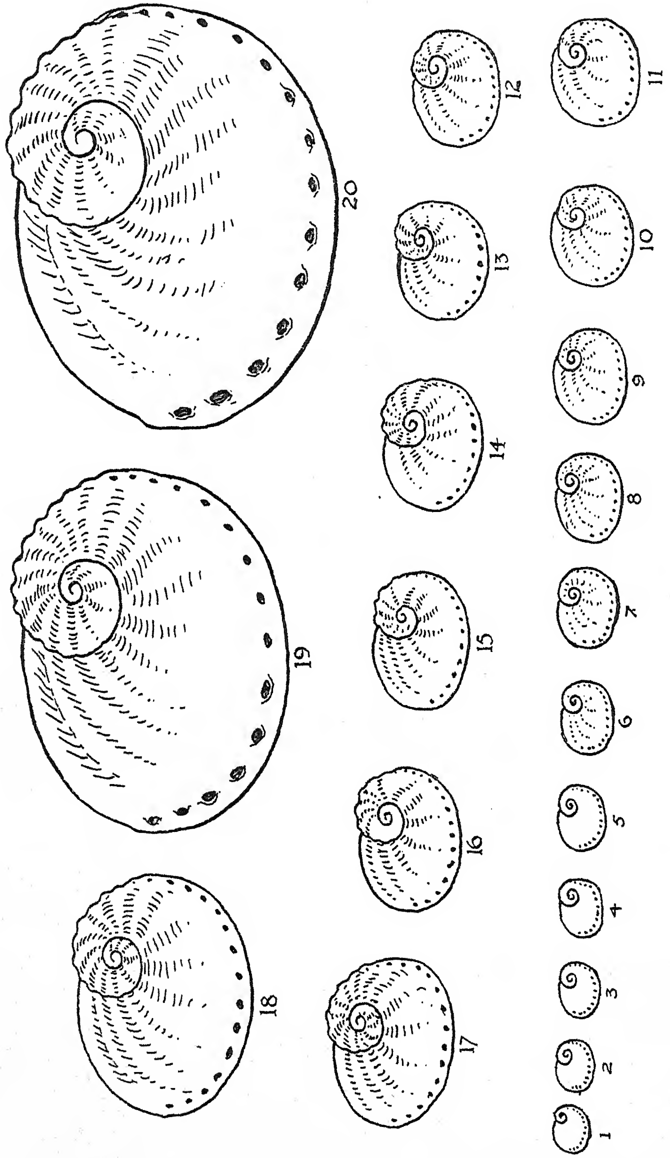


Fig. 2.

Different Stages (1–20) in the Growth of the Ear-shell, Haliotis. From specimens. The marginal apertures, which become increasingly marked, serve for the expulsion of the water used in respiration.

the soil-water. Helped by its chlorophyll, the green plant is able to use part of the energy of the sunlight that bathes its leaves to

build up sugars, starch, and proteins, first of course for its own maintenance and for its growth, thereafter for "reserves", variously stored for its own future, or that of its offspring. On this highly profitable synthesis and storage in the plant, the growth of all animals depends—directly in the case of the sheep and other herbivores, indirectly in the case of the tiger and other carnivores.

Food is thus obviously an indispensable condition of growth; but there are some puzzling cases, e.g. the striking growth behaviour of a single fragment of Planarian worm, without food-canal, and thus incapable of ingesting food; yet soon growing a new head and posterior end, fashioning itself anew into a perfect miniature worm. Here, as in a germinating seed, there must have been absorption of water and utilisation of the previous material in a less condensed form.

Another curious form of growth is expressed in the replacement of lost parts, such as the claw of a crab, or the arm of a starfish;

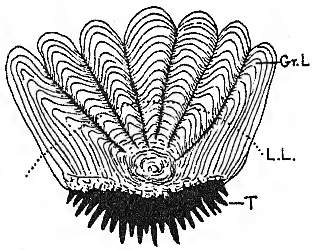


FIG. 3.

Scale of Bony Fish, showing lines of growth (GrL) and the posterior teeth (T). The portion to the convex side of the line LL is overlapped by the scale in front—that is, nearer the head.

and here again the body yields supplies. One of the most extraordinary instances of such replacement-growth is that seen annually when the stag, having dropped his antlers, rapidly grows a new set, which, in the monarch, may weigh seventy pounds!

The great majority of animals have a definite limit of growth, an optimum size, which is normally attained by the adult and rarely exceeded; so there must be some method of growth-regulation. On the other hand, some fishes and reptiles continue growing as long as they live, just like many trees; and this shows that a limit of size is not fundamentally insisted on by nature.

When we think of giants and dwarfs, and of the rarity of their occurrence, the idea of regulation is again suggested. So also when we observe the occurrence—yet rare occurrence—of monstrous growths among animals, we see that growth is essentially a *regulated* increase in the amount of adjustment of living matter. By what

means is such regulation effected? The modern answer to this question is twofold. Regulation is partly due to certain hormones (chemical "messengers") which are produced in "ductless glands" and distributed by the blood. Thus the hormones of the thyroid gland, and those of the pituitary body, have, among other functions, that of growth-control. Again, it has been shown that parts where metabolism is most intense, e.g. the growing point of a stem, exert a sway or dominance over the growth of other parts, as we shall see more fully later.

Another feature of growth is its periodicity. All are familiar with the rings of growth on the cut stem of a tree, which mark its years, through the well-marked seasonal alternation of spring

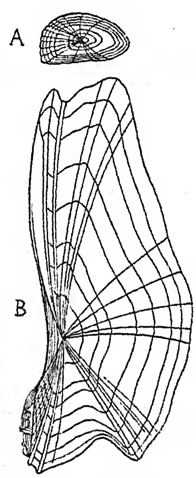


FIG. 4.

A. Section through an Otolith of a Bony Fish, showing the successive lines of deposition.
B. One of the Bones of the Gill Cover or Operculum of the same Fish, showing the successive lines of growth.

and summer wood, which are different in texture. This instance is no exceptional case, but a vivid illustration of the rhythmic periodicity of life. The same is seen in the zoning of fish-scales and the barring of birds' feathers, and in the familiar growth-lines on the shells of the seashore.

Familiarity is apt to dull our eyes to the marvel of growth—the annual covering of the brown earth with verdure; the desert blossoming as the rose; the spreading of the green veil over the miles of woodland; the bamboo rising so quickly that one can see it grow; the Sequoia or Big Tree continuing to increase in bulk for three thousand years; the coral-polyps adding chalice to chalice

till they form a breakwater a thousand miles long; the Arctic jellyfish (*Cyanea arctica*) becoming bigger and bigger till the disc is over seven feet in diameter and the tentacles trail in the waves for over a hundred feet. Again, many an animal egg-cell develops into a body that weighs billions of times as much as its beginning; and this is far exceeded in the growing up of giants—like a Blue Whale, eighty-five feet in length, or an Atlantosaurus with a thigh-bone as high as a tall man.

MULTIPLICATION.—The corollary of growth is multiplication, a term that we are using here in preference to the more general word reproduction, which includes the whole series of functions concerned with giving rise to other organisms. Multiplication essentially means separating off portions or buds, spores or germ-cells, which start a new generation. In the asexual method of separating off large pieces, the connection with growth is obvious; multiplication occurs as a consequence of instabilities which follow overgrowth. As Haeckel said long ago, reproduction is discontinuous growth. Its externally simplest form is seen in the division of an overgrown unicellular organism, yet in the everyday division of most of the cells of plants and animals, this has been elaborated into an intricate process, which secures that each of the two daughter-cells gets a meticulously precise half of everything that is in the parent-cell.

The connection between growth and cell-division is not far to seek. Spencer, Leuckart, and James pointed out independently that as a cell of regular shape increases in volume, it does not proportionately increase in surface. If it be a sphere, the volume of cell-substance or cytoplasm to be kept alive increases as the cube of the radius, while the surface, through which the keeping alive is effected, by various processes of diffusion, increases only as the square. Thus there tends to set in a hazardous disproportion between volume and surface, and this may set up instability. The disturbed balance is normally restored by the cell dividing into two cells. R. Hertwig has pointed out that the nucleus is a dynamic, perhaps trophic, centre to the cell, and that stability depends on keeping up a certain proportion or relation (Kernplasma-Relation) between the nucleoplasm and the cytoplasm. Here again a connection between growth and division is indicated, for if the growth implies an increase of cell-substance out of proportion to nuclear substance, a state of physiological instability may set in, which cell-division may counteract. It is not inconsistent with this that some large cells, like muscle-cells and big Protozoa, become multinucleate; and it may be that some cytoplasmic complications like chromidia (see the chapter on the Cell) may be arrangements for increasing nuclear influence outside the nucleus. The details of ordinary cell-division are in appearance very intricate, but it may

be that the basal fact is a state of "auto-katalysis", or self-fermentation, which automatically follows the disproportionate increase of volume and surface, cytoplasm and nucleoplasm, which persistent growth is apt to induce.

The instability induced by growth may be intracellular, as is familiar in the multiplication of unicellular organisms, or in the ordinary cell-division in many-celled organisms. But it may also take the form of localised lines of weakness or low vitality, as is well seen in the fragmentation of some simple multicellular animals, such as Planarian worms. Along these lines of weakness a process of fission may readily occur.

In cases of sexual reproduction, where germ-cells are separated off to start a new generation, the relation between growth and

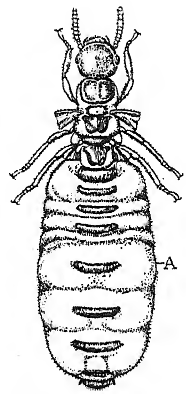


FIG. 5.

Full-grown Queen or Female of a Termite, showing the enormously distended abdomen, containing many thousands of eggs.

multiplication is not, of course, so direct as in cases of asexual reproduction by fission or fragmentation. This will be discussed later on, but it may be pointed out in the meantime that reproduction often occurs at the limit of growth, and that there is a familiar seesaw between feeding and breeding periods, between leafing and flowering, between nutrition and reproduction.

Turning again to the inorganic world, we see a vortex-ring dividing into two, and we know that a molecule often divides into two or more simpler molecules. A nebula may resolve itself into a double star. We must not think of living creatures as though they had no solidarity with Mother Earth. All the inorganic analogies to organic reproduction are interesting. Yet, when all is said, we are left with the conviction that nothing is more distinctive of the organism than its power of multiplying.

The division of a cell is one of the wonders of the world. Bateson wrote (1913, p. 39): "I know nothing which to a man well trained

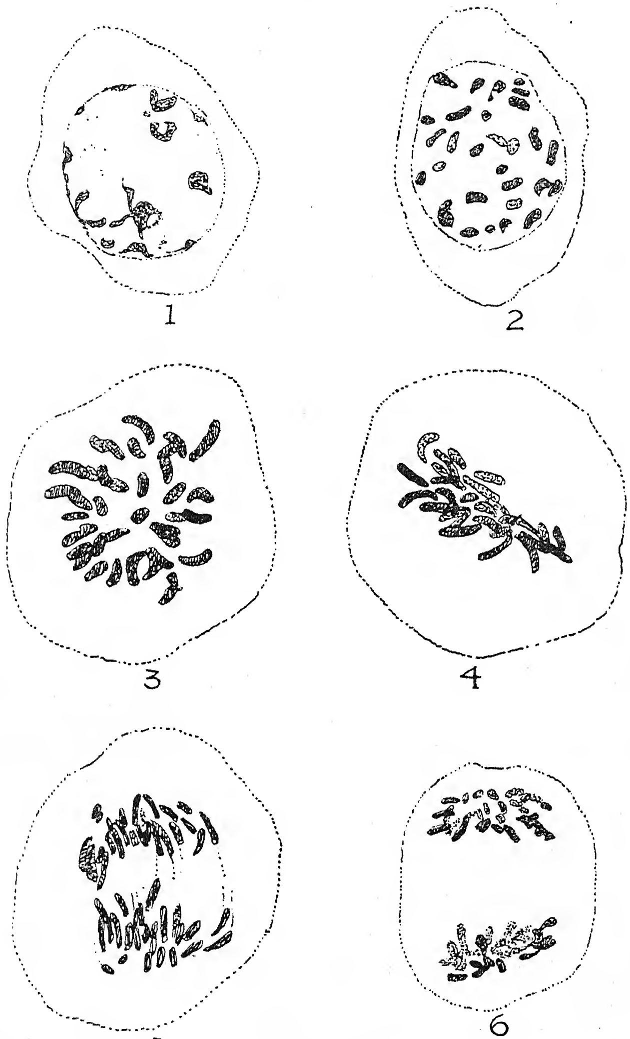


FIG. 6.

The Indirect or Karyokinetic Mode of Cell-division. 1, the resting nucleus with ill-defined chromosomes; 2, the chromosomes well defined; 3 and 4, the chromosomes arranged in an equatorial plane; 5 and 6, the halves of the longitudinally split chromosomes move to opposite poles.

in scientific knowledge and method brings so vivid a realisation of our ignorance of the nature of life as the mystery of cell-division.

. . . It is this power of spontaneous division which most sharply distinguishes the living from the non-living. . . . The greatest advance I can conceive in biology would be the discovery of the instability which leads to the continued division of the cell. When I look at a dividing cell I feel as an astronomer might do if he beheld the formation of a double star: that an original act of creation is taking place before me."

In the present youthful condition of biology it is wise to return at frequent intervals to concrete illustrations. We need the warmth of actual facts to help us to appreciate the quality of reproductivity which we are only beginning to understand. In one day the multiplication of a microbe may result in a number with thirty figures. Were there an annual plant with only two seeds, it could be represented by over a million in the twenty-first year. But a common British weed (*Sisymbrium officinale*) has often three-quarters of a million of seeds, so that in three years it could theoretically cover the whole earth. Huxley calculated that if the descendants of a single green-fly all survived and multiplied, they would, at the end of the first summer, weigh down the population of China. A codfish is said to produce two million eggs, a conger eel ten millions, an oyster twenty millions. The starfish Luidia, according to Mortensen, produces two hundred million eggs every year of its life.

DEVELOPMENT.—In active tissues, like muscle or gland, wear and tear is inevitable, especially in the less labile parts of the cells—the furnishings of life's laboratories, such as the for the most part ultra-microscopic films that partition the cytoplasm into areas. When the results of the wear and tear over-accumulate, they tend to depress activity and in time to inhibit it; and this means ageing, towards death. But this decline of vitality may be counteracted by rejuvenescence-processes in the ageing cells, or by the replacement of worn-out cells by new ones. In some cases the hard-worked cells go fatally out of gear, as in the brain of the busy summer-bee, which does not usually survive for more than six or eight weeks. In other cases, as in ordinary muscle, the recuperation afforded by food and rest is very perfect, and the same cell may continue active for many years. Such cells are comparable to the relatively simple unicellular animals, like the amœbæ, which recuperate so thoroughly that they evade natural death altogether. In another set of cases, e.g. the lining cells of the stomach, or the epithelium covering the lips, the senescent cells die and drop off, but are replaced by others. The outer epidermic layer of the skin (the stratum corneum) is continually wearing away, and as continually being replaced by contributions from the more intensely living and growing deeper stratum (the stratum Malpighii). Similarly at the tip of a rootlet there is a cap of cells which are always dying away and being replaced from the delicate growing point which they protect. From

such replacement of cells there is an easy transition to the re-growth of lost parts. The starfish re-grows its lost arm, the crab its claw, the snail its horn, the earthworm its head. From cells below the plane of separation there is in each case a regulated growth, which replaces what has been lost. We have already mentioned a very striking instance, in which re-growth is normal, and in organic and seasonal rhythm independent of any violence from without—namely, the re-growth which gives the stag new antlers to replace those of the previous year. This capacity for regenerating lost parts is mostly restricted among mammals to superficial structures like hairs; as in the birds to renewing feathers. The reason for this restriction is primarily that highly differentiated cells lose their power of dividing: thus nerve cells are not regenerated in back-boned animals, though when a nerve is cut the fibres, in continuity with the central system, may repair the breakage by sending out delicate processes which feel their way with amœboid tips, towards rejoining the separated portion. Another reason is to be found in the adaptiveness of the regenerative process. As we shall illustrate more fully in the chapter on reproduction, regenerative processes tend to occur in those animals, and in those parts, which, in the natural conditions of their life, are peculiarly liable to recurrent non-fatal injury. In other words, the needful renewal of embryonic tissue is rarely seen, unless there be some recurrent need for it. Most lizards can re-grow their long tail if that has been snapped off by a bird or surrendered in fear or in battle, but the chameleon, which keeps its tail coiled round the branch, has not unnaturally lost this power. Long-limbed animals like crabs, and starfishes with their lank arms, have great regenerative capacity, in striking contrast to the compact and swiftly moving fishes, which cannot even replace a lost scale! The recurrence of non-fatal injuries is not common among the higher animals, so their power of regenerating important parts has waned. Enough of this, however; our present point is that the regeneration of lost parts illustrates a renewal of that regulated growth of complicated structure which is characteristic of embryonic development. Out of apparently simple cells at the stump of a snail's horn, the whole can be re-grown, including the eye at the tip; and this may occur not once only, but forty times. From the broken portion of a Begonia leaf there buds a complete plant—to root and shoot and flower. From such reconstructions there is but a step to the asexual multiplication of many plants and animals—whether by the bulbils of the lily, the budding of the hydra in the pond, or the halving of the planarian worm. When the tail-half of the dividing planarian worm proceeds to differentiate a new head, with brain-ganglia, eyes, and mouth complete, there is an obvious *development*—the formation of new and complex structures out of the undifferentiated and apparently

simple. What we wish to suggest is the consideration of *development* not as necessarily bound up with the making of a new organism along the usual sexual reproduction lines, but as a process linked back from this typical embryonic development to the development of bud and fragment, and thence to the replacement of lost parts, to re-differentiation after de-differentiation, to the mending of wounds—back and back to the self-preservative repair of wear-and-tear effects—back further still to the self-preservative metabolism which we have seen reason to regard as fundamentally characteristic of the organism. Many statements of the characteristic features of an organism have been proposed; we submit that ours is so far unified. For the persistence of intactness leads on to growth, and growth to multiplication, and all three to *development.*

From the days of Aristotle, though often with long interruptions, naturalists have been peering into the common miracle of every-day life—the development of the chick out of a minute clear drop

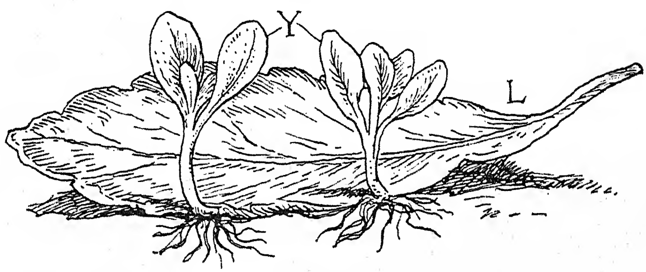


FIG. 7.
Adventitious Buds (Y) Forming at the Sides of a Leaf (L) of *Bryophyllum calycinum.*

of living matter, lying on the top of the yolk of the egg; and though many details of the process are known and some of the factors at work, we still stand amazed at the condensation of individuality into a germ-cell and its re-expression as a young creature. In his 49th Exercitation on "the efficient cause of the chicken", Harvey quaintly expressed, early in the seventeenth century, his sense of the baffling nature of the problem: "Although it be a known thing subscribed by all, that the fœtus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the schools of physicians nor Aristotle's discerning brain have disclosed the manner how the cock and its seed doth mint and coine the chicken out of the egge."

In his discussions of the characteristics of living creatures, Huxley was wont to lay emphasis on what he called "cyclical development". Within the embryo-sac, within the ovule, within

the ovary of the flower, a miniature plant is formed by the division and re-division of the fertilised egg-cell. The ovule becomes a seed; and this, when sown, a seedling. By insensible steps there is fashioned a large and varied fabric, of root and shoot, of leaves and flowers. But sooner or later, after this development is complete, the grass begins to wither and the flower thereof to fade. In the case of an annual plant, there is soon nothing left but the seeds, which begin the cycle anew. It is, Huxley said, "a Sisyphean process, in the course of which the living and growing plant passes from the relative simplicity and latent potentiality of the seed to the full

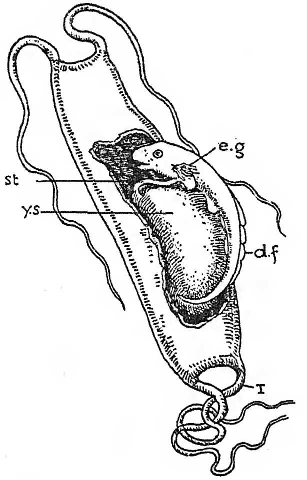


FIG. 8.

Dogfish Egg-case or Mermaid's Purse. From a specimen. The horny shell is drawn out at the four corners into tendrils (T) which automatically moor the egg to seaweed, zoophyte, or the like, thus preventing smothering. The young fish shows the yolk-sac (*ys*) entering the food-canal by a hollow stalk (*st*). On the neck region there are external gills (*eg*); on the back a dorsal fin (*df*).

epiphany of a highly differentiated type, thence to fall back to simplicity and potentiality again."

Similarly, among animals the egg-cell, in many cases microscopic, divides and re-divides, and an embryo is built up. Division of labour sets in among its units, and the structural side of this is differentiation. The hereditary initiatives, implicited in some way that we cannot image, are activated, and out of the apparently simple there emerges the obviously complex. The latent becomes patent, the implicit becomes explicit, the invisible becomes visible. Some cells become nervous, others muscular, others glandular others skeletal; and so the differentiating process continues. Hereditary contributions from parents and ancestors find expres-

sion, some of fundamental importance and others relatively trivial; the past lives on in the present; often the individual shows, in varying degree, evidence that it is "climbing up its own genealogical tree". Sometimes the embryo develops steadily and directly into the likeness of its kind, as in birds and mammals, with only traces of circuitousness, such as notochord and gill-clefts disclose—tell-tale evidence of the lien the past continues to hold on the present.

In many other cases development is anything but direct, for there is an interpolation of larval stages, often in marked adaptation to difficult circumstances. Thus frogs and toads, the modern representatives of an epoch-making colonisation of the dry land in the late Devonian period, have not freed themselves from the ancestral method of liberating the eggs in the water, a relatively much safer cradle than terra firma can afford. The prolonged tadpole stages imply a continuance of the development in comparative safety, and what leaves the water is a fully formed air-breathing miniature of the adult frog. The caterpillar is a voraciously feeding and rapidly growing larval form, accumulating stores of energy, which are partly used in the re-building that follows down-breaking in metamorphosis, yet leave enough over to enable the butterfly to lead its joyous life, with little in the way of nutritive exertion, up to its fatal climax of reproduction. But in all cases, however diverse in detail, development is the progressive attainment of full-grown complexity from comparatively undifferentiated simplicity, and there is no characteristic of the living organism more distinctive than this.

BEHAVIOUR, REGISTRATION, AND EVOLUTION.—A third triad of qualities which are distinctive of the living organism may be summed up in the words behaviour, registration, and evolution, in which as in previous triads an underlying unity may perhaps be discerned.

BEHAVIOUR.--Herbert Spencer spoke of life as "effective response", and from the amœba upwards we recognise among animals the power of linking actions in a chain so that the result is behaviour—always purposive and in the higher reaches purposeful. Responses are common in the inorganic world—from gentle weathering to volcanic explosion—but non-living things do not show the living creature's power of reacting in a self-preservative way. Among plants, for various reasons, such as the fixed habit of the great majority and the enclosing of the cells in cellulose, there is relatively little exhibition of that purposive "doing of things" which we call behaviour, but we must not forget the insurgent activities of climbing plants or the carnivorous adventures of Venus's Fly-trap and the Sundew. An entire section of this book is devoted to illustrating the long inclined plane of behaviour.

ENREGISTRATION.—A bar of iron is never quite the same after it has been severely jarred; the "fatigue of metals" is one of the serious risks of engineering; the violin suffers from mishandling. But these are hardly more than vague analogies of the distinctive power that living creatures have of enregistering the results of their experience, of establishing internal rhythms, of forming habits, and of remembering. As W. K. Clifford put it: "It is the peculiarity of living things not merely that they change under the influence of surrounding circumstances, but that any change which takes place in them is not lost, but retained, and, as it were, built into the organism, to serve as the foundation for future action." We are not anticipating the question of the possible entailment of individual acquisitions or modifications; we are in the meantime keeping to the fact that the way in which an organism reacts to stimuli is determined not only by the innate constitution, but also by the accumulated experience of the whole and of the parts during the individual lifetime. In various forms this is a distinctive feature of the living creature.

EVOLUTION.—In the attempt to understand organisms we must envisage them as a whole, we must see them in the light of evolution. Thus it must be recognised as characteristic of organisms that they give origin to what is new; they have evolved and evolution is going on. There is variability in the crystalline forms which the same substance may assume; the modern physicist tells us of "isotopes" like the different kinds of "lead", which have the same chemical properties, yet differ in the structure of the nucleus of their atoms; the modern chemist even assures us of the transmutation of elements, thus not a little justifying the medieval alchemists' dream and quest. The synthetic chemist shuffles but a few molecules, seldom going beyond Carbon, Hydrogen, Oxygen, and Nitrogen, and yet creates long successions of new dyes and drugs, new perfumes and explosives. Yet these are only suggestive analogies; for the living organism is the supreme, though unconscious, creative chemist.

No doubt there are species that show nowadays little or no variation; there are conservative living types that seem to have remained the same since their remains were first buried in the mud millions of years ago, as in the case of the Cambrian Lampshell Lingula, the Silurian Nautilus, and the Triassic lung-fish Ceratodus; but the larger fact is variability. In multitudes of cases the offspring show something new.

What impressions of variability we get at a "show"—whether of dogs or pigeons, roses or pansies! Here we have, as it were, the fountain of life rising high in the air—blown into strange forms by the breeze, yet modulated, to its own ceaseless waxings and wanings, by varying pressures from its source. Two hundred different

"forms" or varieties are described by Jordan in one of the commonest of small Crucifers, the whitlow-grass or *Draba verna*; and these are no longer fluctuating but breeding true. Again, Lotsy speaks of the bewildering diversity exhibited by a series of about two hundred specimens of the Common Buzzard (*Buteo buteo!*) in the Leyden Museum, "hardly two of which are alike". It is difficult to see much difference between one reeve and another, but it is as difficult to find two ruffs that look alike! Whenever one settles down to work at species, one is confronted with the difficulty that so many of them are in flux. Yet others again seem to have settled down in unchanging stability.

The facts and factors of organic evolution will be discussed in

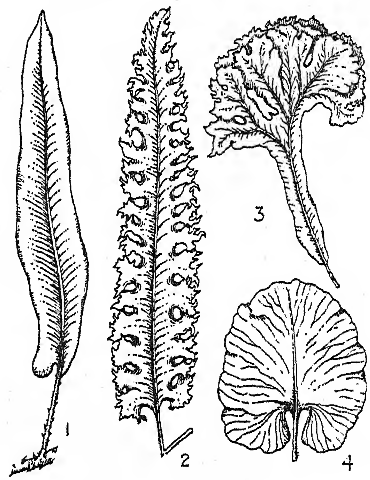


Fig. 9.
Three Mutations of the Frond in the Hart's Tongue Fern (*Scolopendrium vulgare*). 1. The normal type. After Lowe.

their proper place, here we are only concerned with pointing out that variability—and with it evolvability—must be ranked as one of the fundamental characteristics of living beings.

Whatever theory we hold as to the factors of organic evolution, we must leave room for the bent bow of endeavour. The organism selects stimuli from its environment and often moves from one environment to another; the organism is often experimental, moulding itself by its efforts; the organism tests the newnesses of its inheritance in its ceaseless trafficking with circumstances. The organism is what some have called a "historic being", meaning that it comes into existence with an inheritance of organisation and impulses—a rule of life, what from Plato's time has been

thought of as "a conformity with plan". The chemical individuality of the proteins in each species is one expression of this, and so is the nature of the chromosomes. But besides these and other physical features there is the psychical individuality, certainly not less real; the organism is a psycho-physical being. This is the thread that runs through all the triads, the last three in particular. As von Uexküll says in his *Theoretical Biology*: "there is a non-material order which first gives to matter its framework—a rule of life. . . . It is like a melody, which controls the sequence of sound and the rhythm in accordance with law, but becomes apparent only as it becomes operative, and then takes on the tone-colour which the properties of the particular instruments bestow on it." Perhaps these metaphors do not help us much, but in the meantime, awaiting discussion in the body of the book, we wish merely to state our conviction that the mental activity (of memory and feeling, as well as of intelligence), which becomes indisputable in the higher animals, is struggling for expression throughout. Perhaps this is the central secret of life?

SUMMARY OF THE CHARACTERISTICS OF THE ORGANISM

(A) In spite of continuous chemical and physical flux there is in the organism a persistence of intactness or integrity for a longer or shorter period. This is associated with the anabolic processes that counterbalance the katabolic, with the repair that counteracts waste, with the rejuvenescence that wards off senescence. This self-preservation is associated with the dominance of proteins, which have large complex molecules, representing an accumulation of potential chemical energy. But these proteins are always in a colloidal state, which admits of intensity and rapidity of chemical reactions on the surfaces of the multitudinous particles or droplets. Each type of organism has probably some unique protein of its own—there is chemical individuality. Thus under the general quality of persistence amid unceasing metabolism, there is a triad of facts: (1) the upbuilding and downbreaking of proteins, (2) their occurrence in the colloidal state, and (3) their specificity.

(B) The second triad of qualities includes the organism's characteristic powers of growing, multiplying, and developing. A surplus of income over expenditure is the primal condition of organic growth. The organism's growth, as contrasted with that of a crystal, is at the expense of materials more or less different from those of the growing body; it implies active assimilation, not passive accretion; and it is a very definitely regulated process.

Growth naturally leads to the simpler forms of multiplication

or reproduction, for in simple cases persistent growth tends to bring about instability, which may be intracellular as in unicellular organisms and in ordinary cell-division, or localised along a line of weakness or low vitality, as in the fragmentation of some of the simple multicellular animals.

Development is the progressive attainment of full-grown complexity from comparatively undifferentiated simplicity, be this in stump or fragment, leaf or bud, or as spore and germ-cell. It implies an expression of hereditary initiatives in appropriate nurture, and often in such a way that the individual stages can be correlated with great steps in the racial history.

(C) Living creatures are contrasted with non-living things by their purposive behaviour, by their power of enregistering their experiences, and by their capacity for giving rise to the new. Finally, since the mental activity of living creatures becomes indisputable in the higher forms, we can hardly resist the conclusion that this aspect is struggling for expression throughout. The organism is a psycho-physical being.

GLIMPSES OF LIFE

Our discussions of living creatures are apt to be too abstract and cold; we lose the feeling of the mysterious which all life should suggest. In our inhibiting conventionality we run the risk of false simplification. Therefore, at the risk of a little repetition, we devote the rest of this introduction to what might be called "glimpses of life"—the contrast between the living creature and a crystal, the quality of vital insurgence, the fact of organic beauty, and, more generally, the ever-widening and deepening wonder of the world.

CRYSTALS AND ORGANISMS.—When Linnæus wrote his famous, yet now partly outworn, aphorism, "Stones grow; Plants grow and live; Animals grow and live and feel", he must have been thinking of crystals. For ordinary stones do not grow—except smaller; whereas crystals afford beautiful illustrations of increase in size. Suppose, says Sir William Bragg in his luminous lectures "Concerning the Nature of Things" (1925), the crystallographer wishes to get a fine big crystal of common salt, he suspends a minute, well-formed crystal in a solution of brine at a concentration just ready to form a salt precipitate. That is step one. He also makes sure of a certain temperature, which he knows from previous experience to be suitable to tempt the atoms of sodium and chlorine to give up their freedom "when they meet an assemblage of atoms already in perfect array—that is to say when they come across a suspended crystal". Sometimes the solution is kept in gentle

movement so that various parts of it get a chance of meeting the nucleus, which, so to speak, tempts them to settle down—freezing into architecture. Into the physics of this we need not here enter; our point is simply that in a suitable environment, with time and quiet, a crystal-unit "grows". By accretion it becomes a handsome large crystal. On to its faces other crystal-units are added, and on the new faces more again, until there is formed—an edifice. A distinction must be made between the molecule, say of silicon-dioxide (SiO_2), and the crystal-unit of quartz, which consists of three molecules of silicon-dioxide, arranged in some screw-like way; so here already we see conditions of variability.

The crystal increases in size in an orderly way; how does this differ from the growth of an animal or a plant? Is there a real resemblance, or is it a misleading analogy? The first answer is that a crystal increases in size at the expense of material, usually a solution, that is chemically the same as itself; whereas animals and plants feed on substances different from their own living matter—often very different. This is sound commonsense, and yet the edge is taken off it a little by two facts, first that it is possible to feed an amœba on amœbæ, or a tadpole on tadpoles, or a rat on rats; and, secondly, it is possible to increase the size of a crystal when it is placed in a solution of a chemically different substance, which has, however, the same form of crystallisation.

Then one might lay emphasis on the fact that the increase in the size and weight of a crystal is by accretion from without, whereas organisms grow by taking in raw materials, altering these, and building from within. In the growth of seeds and eggs and the like, there is obviously a utilisation of a previously accumulated store of condensed food. We see then that the crystal grows from without, by the addition of new crystal-units on the faces of those already existing, whereas organisms grow from within.

But there is another, more general, way of looking at the difference between crystal increase and organic growth: the one is passive and the other is active. It is not so much that the crystal grows, as that it is added to by other crystal units—usually, moreover, in saturated solution. But an organism actively takes in its food, actively changes and distributes it, and actively builds with it.

But some authorities who press the analogy between crystals and creatures bring forward another supposed resemblance. If a crystal is broken there is a neat mending, provided there is the proper environment. There is more rapid accretion at the broken surface than elsewhere; the repair is often in proportion. This is very suggestive of the way in which an animal or a plant replaces a lost part or repairs an injury. If a crystal be broken into two, each half may form a perfect whole. If a Planarian worm or a Hydra be cut across, each half usually "regenerates" an entire

animal. But the crystal's "regeneration" is passive, from without, and homogeneous; that of the organism is active, from within, and heterogeneous.

Another supposed resemblance that has been emphasised is the power of lying latent that may be seen in crystal and creature alike. The seed of a plant may remain dry for a decennium, but sow it and it will germinate. The egg or the half-developed embryo of an animal may lie unchanged for many years, but give it the appropriate environment and it will resume its activity. Entire animals like "vinegar-eels" may remain without hint of life for many years; but it is only necessary to put them in their proper surroundings to see them revive and multiply. Everyone knows how the spores of microbes may lie low for a long time and be blown about by the wind, but let one light on a suitable medium and it reasserts its power—perhaps its virulence to our undoing.

Now it is a similar power of lying latent that enthusiasts claim for crystals. Thus Dr. A. E. H. Tutton, one of the leading authorities, says: The virility of a crystal is unchanged and permanent. He pictures very vividly what may happen to a crystal of quartz detached by the weathering of a piece of granite thousands of years ago. It may be "subsequently knocked about the world as a rounded sand grain, blown over deserts by the wind, its corners rounded off by rude contact with its fellows, and subjected to every variety of rough treatment". But if it happen in our own day to "find itself in water containing in solution a small amount of the material of which quartz is composed, silicon-dioxide, it will begin to sprout and grow again". From a grain of sand in such conditions several typical crystals of quartz may grow out in different directions. "This marvellously everlasting power possessed by a crystal, of silent imperceptible growth, is one of the strangest functions of solid matter, and one of the fundamental facts of science which is rarely realised, compared with many of the more obvious phenomena of nature."

But Dr. Tutton chose a very resistant crystal; what he says of the crystal of quartz would not be so true of a crystal of common salt, just as what we said of the vinegar threadworm would not hold for the earthworm. When atoms are very firmly locked together in an intricate space-lattice system we do not expect them to be changeful. It is not easy to induce a diamond to change its state. But the persistence of some organisms through years of latent life is much more remarkable, for they often become dry and brittle, and thus pass out of the colloidal state which is characteristic of living matter. Yet they do not die. As for the prolonged persistence of some organisms when they are not in a latent state, the marvel there is that they retain their intact integrity in spite of the ceaseless internal bustle of metabolism. *Plus ça change, plus c'est la même chose.*

It is certainly a noteworthy fact that many kinds of crystals, not larger than bacteria, float about in the air as microbes do. And just as a microbe may set up a far-reaching change when it lights on a suitable medium, so a microscopic crystal landing in a solution which is in a properly receptive condition may set up crystallisation. But the differences seem to us to be greater than the resemblances; for the minute crystal is but a passive peg to which molecules attach themselves, while the microbe is an active agent that attacks the medium and fills it with its progeny.

No one wishes to think of living creatures as if they had not antecedents in the non-living world. Science is not partial to Melchizedeks. On the other hand, we hold to the apartness and uniqueness of life. Dr. A. E. H. Tutton begins his fine book on *The Natural History of Crystals* (London, 1924), by saying that no definition of life has yet been advanced that will not apply equally well to crystals, but we have given reasons for not accepting this statement. The living creature's growth, repair, and reproduction are very different from those of crystals; life is an enduring activity, persisting in spite of its metabolism; the organism enregisters its experience and acts on its environment; it is a masterful, even creative, agency. The crystal, especially the gem, is a new synthesis, compared with the disarray of the dust; the organism is another and on a different line.

THE INSURGENCE OF LIFE.—It is difficult to find the fit word to denote that quality of irrepressibility and unconquerability which is characteristic of many living creatures. There are some, no doubt, that drift along, but it is much more characteristic to go against the stream. Life sometimes strikes one as a tender plant, a flickering flame; and who can forget that one of the Ephemerides or mayflies has an aërial life of but a single hour! At other times, the impression we get is just the opposite, for the living creature often shows itself tenacious, tough, and dogged. In his admirable *Introduction to the Study of Trees* (Home Univ. Library, 1927), Dr. Macgregor Skene of Bristol University mentions that three carefully measured stumps of the "big tree", *Sequoia gigantea,* of California showed rings going back to 1,087, 1,122, and 1,305 years B.C. The actual record for the second tree was 2,996 years and for the third 3,197, without allowing for some rings that have been lost in the centre. A specimen of the dragon-tree on Teneriffe is supposed to be 6,000 years old, and a bald cypress near Oaxaca in Mexico, 110 feet high with a circumference of 107 feet at breast height, is credited with over 6,000 years. As these giants are still standing, their longevity is *inferred,* whereas that of the felled Sequoias is proved by the ring counts. But, in any case, there is astounding tenacity of life, and, without going

out of Britain, we may find other impressive illustrations. For, as Dr. Skene says, "it is quite certain that we have many oaks which have passed their thousand years, and some which may be much older".

Another way of looking at the insurgence of life is to think of some of the extraordinary haunts which many living creatures have sought out. Colonel Meinertzhagen, speaking recently of the lofty Tibetan plateau, directed attention to the herds of antelopes and kiangs (wild ponies) that seem to be able to thrive on next to nothing! The explorer marked out with his field-glass an area where he saw a small herd of kiangs feeding, and then visited the spot. Measuring a space one hundred yards by ten, he gathered up

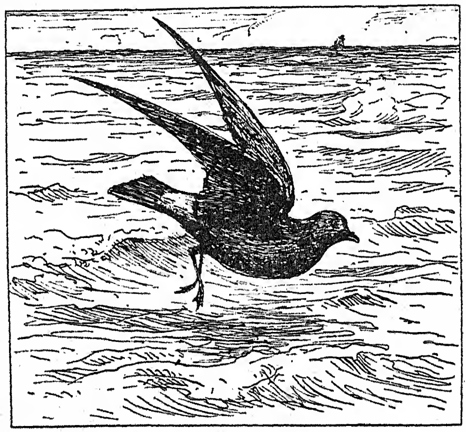


FIG. 10.
The Storm-Petrel (*Procellaria pelagica*), the smallest web-footed bird, just over six inches in length, which is at home on the open sea, and rarely touches land except at the nesting-time.

every scrap of vegetation, and the result was a quaint collection—seventeen withered blades of coarse grass and seven small alpines—not enough to feed a guinea-pig! Of course, the kiangs had been there before him, but there was little but very frugal fare all around. Meinertzhagen, to whom we owe much information on the altitude of bird flight, saw a flock of swifts at 18,800 feet. At 19,950 feet he shot a raven which showed undue inquisitiveness as to his movements; at 21,059 feet, the highest point reached, he found a family of wall-creepers—dainty little refugees of the mountains. Facts like these must be taken into consideration in our total conception of life, for they are surely as essential to the picture as the semi-permeability of the cell-membrane, or any other fundamental fact of life-structure. No doubt hunger is a sharp spur; the impelling

power of the struggle for existence cannot be gainsaid; but we cannot get away from the impression that we must also allow for something analogous to the spirit of adventure. At all events, the facts show that while the environment selects organisms, often winnowing very roughly, there are other cases where organisms select their environment, and often adventurously. There is a quality of tentativeness in many organisms, that look out not merely for niches of opportunity into which to slink, but for new kingdoms to conquer.

THE FACT OF BEAUTY

No one who studies Animate Nature can get past the fact of Beauty. It is as real in its own way as the force of gravity. It used to be spoken of as though it were a quality of the exotic—of the Orchid and the Bird of Paradise—now we feel it most at our doors. St. Peter's lesson has been learned, and we find naught common on the earth. As one of our own poets has said: Beauty crowds us

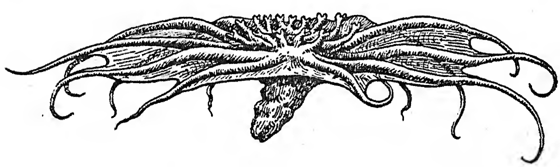


FIG. 11.
A Pelagic Holothurian (*Pelagothuria ludwigi*). After Chun. Unlike the typical forms, it is lightly built and adapted for open-sea life.

all our life. We maintain that all living things are beautiful; save those which do not live a free life, those that are diseased or parasitised, those that are half-made, and those which bear the marks of man's meddling fingers—monstrosities, for instance, which are naturally non-viable, but live a charmed life under human protection. With these exceptions all living creatures are beautiful, especially when we see them in their natural surroundings. To those who maintain that Animate Nature is spotted with ugliness, we would reply that they are allowing themselves to be preoccupied with the quite exceptional cases to which we have referred, or that they are unable to attain the detachment required in order to appreciate the esthetic points of, say, a snake or any other creature against which there is a strong racial or personal prejudice. To call a jellyfish anything but beautiful is either a confusion of thought or a submission to some unpleasant association, such as being severely stung when bathing. That there are many quaint, whimsical, grotesque creatures must be granted, to which conventionally minded zoologists who should have known

better have given names like *Moloch horridus*, but we have never found any dubiety in the enthusiasm with which artists have greeted these delightfully grotesque animals; and the makers of beauty surely form the court of appeal for all such cases.

When we say that all free-living, fully formed, healthy living

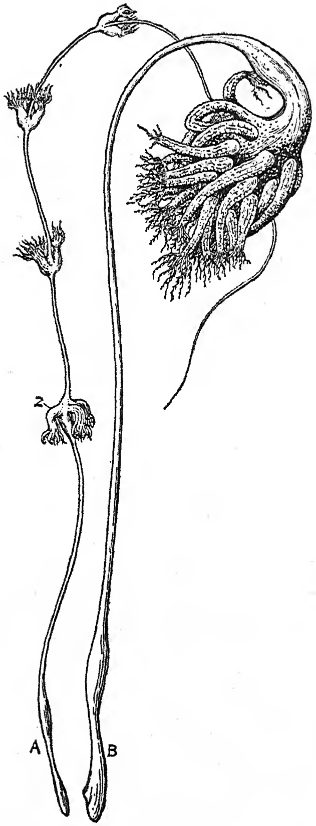


FIG. 12.

Two Deep-sea Pennatulids, Chunella (A), and Umbellula (B). From specimens. They show respectively terminal and distantly separated groups of polyps, raised on long stalks above the ooze in which the sterile base is embedded.

creatures are beautiful, we mean that they excite in the spectator the characteristic kind of emotion which is called esthetic. The thing of beauty is a joy for ever. The esthetic emotion is distinctive; it brings no satiety; it is annexed to particular qualities of shape, colour, and movement; it grows as we share it with others; it grips us as organisms, body and soul, and remains with us incarnate.

Why should the quality of exciting this distinctive emotion be pervasive throughout the world of organisms, as compelling in new creatures which the human eye never saw before as in the familiar favourites with which our race has grown up? It is possible that some light is thrown on this question when we analyse the esthetic delight which every normally constituted man feels when he watches the Shetland ponies racing in the field, the kingfisher darting up the stream like an arrow made of a piece of rainbow, the mayflies rising in a living cloud from a quiet stretch of the river, or the sea-anemones nestling like flowers in the niches of the seashore rocks. The forms, the colours, the movements, set up agreeable rhythmic processes in our eyes, agreeable rhythmic messages pass to our brain, and the good news—the pleasedness—is echoed throughout the body, in the pulse, for instance, and in the beating of the heart, as Wordsworth so well knew. The esthetic emotion is certainly associated with a pleasing bodily resonance; in other words, it has its physiological side. The second factor in our esthetic delight is perceptual. The "form" of what we contemplate is significant for us and satisfies our feeling. The more meaning is suffused into the material, the more our sense of beauty is enhanced. The lines and patterns and colours of living creatures go to make up a "form" which almost never disappoints. And in spite of some experts who maintain that nothing which does not appear can count in the esthetic impression, we agree with that thoughtful physiologist, Sir John Burdon Sanderson, who was persuaded that certain associated concepts, such as that of adaptiveness, have considerable influence in our esthetic enjoyment of animal form and structure, even when the ideas simply remain in the background of the mind.

But is there any particular reason why animals and plants should delight us so uniformly, should give us esthetic pleasure with more infallibility and convincingness than human creations or inanimate objects do? It has been known for centuries, and it has been borne out by experiments with children, that certain forms and patterns, as well as colour-combinations, are much more pleasing than others. There are lines that flow and shapes that sing. Why should there be among living creatures such a practical omnipresence of pleasing lines and colours? Must not part of the answer be that natural creatures are harmonious unities which have stood the test of time, which have been chiselled from within by harmonious metabolism and rhythmic orderly growth? Perfectly adaptive architecture from which all the useless has been eliminated, the organised ripple-marks of orderly regulated growth, the colour-expressions of successfully rhythmic metabolism from which everything disorderly has been sifted out, *ought* to be beautiful; that is to say, they may be expected to excite pleasant physio-

logical processes in the spectator. Did not Meredith put the idea in a nutshell when he said: "Ugly is only half-way to a thing"? There is almost no ugliness in Animate Nature because the lines and colours, in their arrangements and combinations, are the expression of unified, viable, well-sifted individualities which have stood the test of ages of selection. Has not Benedetto Croce defined beauty as "successful expression"? In the age-long struggle for existence, the inharmonious, the "impossible", have been always weeded out before they took firm root and multiplied. The monster is a contradiction in terms. Nature pronounces her verdict on ugliness by eliminating it. Beauty is Nature's stamp of approval on harmonious viable individuality. Unpleasing lines are to the eye what discords are to the ear: they ask of us what is out of order and out of tune. Human combinations of colours may be ugly, and almost as painful as noises. They ask the "impossible" from our retina. But such unpleasant colour-schemes never occur in wild nature, for that would mean a contradiction in terms. Even when organic colours are due to waste products, as may be the case in withered leaf or butterfly's wing, there is "beauty for ashes".

More than one naturalist has suggested a further step, that to our primary sensory delight, with its perceptual appreciation of significance, there is often added an associated *idea* that thrills us with pleasure. This may be best illustrated, perhaps, in reference to what animals make outside of themselves, though it applies also to their use of materials within themselves. When we study the nests of birds, the webs of spiders, the combs of bees, the encasements of some arenaceous Foraminifera, and so on, we recognise great effectiveness in the use of materials, or a selection of fit and congruent components, or a triumphing over technical difficulties, or an expression of individuality sometimes touching the confines of art. Then in a new way deep calls to deep, we have a sympathetic joy in the creature's mastery of its materials and circumvention of difficulties. We enjoy a vicarious victory of mind or life over matter. We suggest for consideration the general conclusion that all free-living, full-grown, wholesome organisms have the emotion-exciting quality of beauty. And is not our humanly sympathetic appreciation of this protean beauty of the world inherent and persistent in us as also part of the same world of life, and evolved far enough to realise it more fully, communicate it to each other more clearly?

THE WONDER OF THE WORLD

Aristotle, who was not unaccustomed to resolute thinking, tells us that throughout nature there is always something of the wonderful—*thaumaston*. What precisely is this "wonderful"? It

cannot be merely the startling, as when we announce the fact that if we could place in one long row all the hair-like vessels or capillaries of the human body, which connect the ends of the arteries with the beginnings of the veins, they would reach across the Atlantic. It would be all the same to us if they reached only half-way across. Nor can the wonderful be merely the puzzling, as when we are baffled by the "sailing" of an albatross round and round our ship without any perceptible strokes of its wings. For some of these minor riddles are being read every year, without lessening, however, the fundamental wonderfulness of Nature. Indeed, the much-abused word wonderful is properly applied to any fact the knowledge of which greatly increases our appreciation of the significance of the system of which we form a part. *The truly wonderful makes all other things deeper and higher.* Science is always dispelling mists—the minor marvels; but it leaves us with intellectual blue sky, sublime mountains, and deep sea. Their wonder appears—and remains.

There seems to be a rational basis for wonder in the abundance of power in the world—the power that keeps our spinning earth together as it revolves round the sun, that keeps our solar system together as it journeys through space at the rate of twelve miles a second towards a point in the sky, close to the bright star Vega, called "the apex of the sun's way". At the other extreme there is the power of a fierce little world within the complex atom, whose imprisoned energies are set free to keep up the radiant energies of sun and star. And between these extremes of the infinitely great and the infinitely little are the powers of life—the power of winding up the clock almost as fast as it runs down, the power of a fish that has better engines than those of a *Mauretania*, life's power of multiplying itself, so that in a few hours an invisible microbe may become a fatal million.

Another, also old-fashioned, basis for wonder is to be found in the immensities. It takes light eight minutes to reach us from the sun, though it travels at the maximum velocity—of about 186,300 miles per second. So we see the nearest star by the light that left it four years ago, and Vega as it was twenty-seven years ago, and most of the stars that we see without a telescope as they were when Galileo Galilei studied them in the early years of the seventeenth century. In any case it is plain that we are citizens of no mean city.

A third basis for rational wonder is to be found in the intricacy and manifoldness of things. We get a suggestion of endless resources in the creation of individualities. Over two thousand years ago Aristotle knew about five hundred different kinds of animals; and now the list of the named and known includes twenty-five thousand different kinds of backboned animals, and a quarter of a million—

some insist on a minimum of half a million—backboneless animals, each itself and no other. For "all flesh is not the same flesh, but there is one kind of flesh of men, another flesh of beasts, another of fishes, and another of birds". The blood of a horse is different from that of an ass, and one can often identify a bird from a single feather or a fish from a few scales. One is not perhaps greatly thrilled by the fact that the average man has twenty-five billions of oxygen-capturing red blood corpuscles, which if spread out would occupy a surface of 3,300 square yards; but there is significance in the calculation that he has in the cerebral cortex of his brain, the home of the higher intellectual activities, some nine thousand millions of nerve cells, that is to say, more than five times the present population of the globe—surely more than the said brain as yet makes use of.

So it must be granted that we are fearfully and wonderfully made! Our body is built up of millions of cells, yet there is a simplicity amid the multitudinousness, for each cell has the same fundamental structure. Within the colloid cell-substance there floats a kernel or nucleus, which contains forty-seven (or in woman forty-eight) chromosomes, each with a bead-like arrangement of smaller microsomes, and so on, and so on. Similarly, while eighty-nine different elements have been discovered out of the theoretically possible ninety-two, we know that they differ from one another only in the number and distribution of the electrons and protons that make up their microcosmic planetary system. What artistry to weave the gorgeously varied tapestry of the world out of two kinds of physical thread—besides, of course, Mind, which eventually searches into the secret of the loom.

A fourth basis for rational wonder is in the orderliness of Nature, and that is almost the same thing as saying its intelligibility. What implications there are in the fact that man has been able to make a science of Nature! Given three good observations of a comet, the astronomer can predict its return to a night. It is not a phantasmagoria that we live in, it is a rationalisable cosmos. The more science advances, the more the fortuitous shrivels, and the more the power of prophecy grows. Two astronomers foretold the discovery of Neptune; the chemists have anticipated the discovery of new elements; the biologist can not only count but portray his chickens before they are hatched. The Order of Nature is the largest of all certainties; and leading authorities in modern physics tell us that we cannot think of it as emerging from the fortuitous. It is time that the phrase "a fortuitous concourse of atoms" was buried. Even the aboriginal nebula was not *that*! No doubt there have been diseases and tragedies among men, cataclysms and volcanic eruptions upon the earth, and so on—no one denies the shadows; but even these disturbances are not disorderly; the larger

fact is the absence of all caprice. To refer to the poet's famous line, no one any longer supposes that gravitation can possibly cease when he goes by the avalanche. Nor will a microbe's insurgence be influenced by the social importance of the patient.

Corresponding to the intelligibility of Nature is the pervasiveness of beauty—a fifth basis of rational wonder, appealing to the emotional side of our personality; but we have discussed this a little in a previous section. Surely Lotze was right, that it is of high value to look upon beauty not as a stranger in the world, nor as a casual aspect of certain phenomena, but as "the fortunate revelation of that principle which permeates all reality with its living activity".

A sixth basis of rational wonder, particularly relevant here and already illustrated, is to be found in the essential characteristics of living creatures. We need only add the caution that the marvel of life is not to be taken at its face value; as Coleridge wisely said, the first wonder is the child of *ignorance*; we must attend diligently to all that biochemistry and biophysics can discount; we must try to understand all that can be formulated in terms of colloids, and so on. Yet when all that is said, there seem to be large residual phenomena whose emergence in living creatures revealed a new depth in Nature. Life is an enduring, insurgent activity, growing, multiplying, developing, enregistering, varying, and above all else evolving.

For this is the seventh wonder—Evolution. It is not merely that all things flow; it is that life flows uphill. Amid the ceaseless flux there is not only conservation, there is advancement. The changes are not those of a kaleidoscope, but of "an onward advancing melody". As the unthinkably long ages passed the earth became the cradle and home of life; nobler and finer kinds of living creatures appeared; there was a growing victory of life over things and of "mind" over "body"; until at last appeared Man, who is Life's crowning wonder, since he has given to everything else a higher and deeper significance. And while we must consider man in the light of evolution, as most intellectual combatants admit, there is the even more difficult task of envisaging evolution in the light of Man. *Finis coronat opus*—a wise philosophical axiom; and yet the scientist must qualify it by asking who can say Finis to Evolution.

CHAPTER II

ECOLOGICAL

ECOLOGY AND ITS SIGNIFICANCE.—The historic progress of the biological sciences has essentially been made by breaking away from and beyond the old "natural history" of animals and plants, as from Pliny onwards to Buffon. It was full time to settle down to ever keener and more thoroughgoing scrutiny of the organisms concerned; first, therefore, descriptively but anatomically also. And thus with the great result, through comparative anatomy, of advance towards more and more orderly classification of them, as from Linnæus to Jussieu and De Candolle, to Cuvier and thence onwards, and with study of past forms enriching and advancing classification.

It was, of course, seen—and by physicians apparently first—that it is not enough to observe, analyse, and compare structures: their working uses, their functions, must be searched into and understood: so physiology has advanced, and goes on increasingly. Development also presents its fascinating riddles; and first as observation, as scrutiny of forms in origin and change, from simple and general to complex and particular; and next as endeavour to comprehend the functional processes of growth and development throughout these phases. With all these sub-sciences in advance, the times were obviously ripening for speculation and inquiry as to origins. Thus the long succession, from eighteenth-century evolutionists to Lamarck's doctrines, and through a later generation and more to Darwin, with his well-marshalled evidence for organic evolution, and his luminous doctrine of natural selection as main agency for its advance.

In course of this progress, most active and productive biologists have substantially lost touch with the old natural history, and often even interest in it, their whole powers and time being more profitably concentrated on their particular lines and groups of inquiries; and such specialised studies, of course, have been needed more than ever since Darwin's epoch-making days, in keeping with the advance of physical and chemical science. Yet with due respect for their various lines of inquiry, and here with utilisation of their results as far as space allows, this is the place to ask: To what purpose all these inquiries, into structure and functions, and their development, to their utmost specialism? Towards what application do all these general conceptions lead, as of the classification and distribution of life-forms, present and past; and even of all we can make out of their evolution?

In short, what shall we do with all this hard-won knowledge, both particular and general; which we have reached through escaping from the simple and crude old naturalistic story-telling of animal ways and plant wonders?

And the answer to this question—is it not to apply all we have learned, are learning, and can learn—and in each and all these ways, analytic and synthetic, structural and functional, and thus developmental and evolutionary—to Life's actual ways and concrete wonders once more? In fact, to bring them back to Natural History, now upon its modern spiral of never altogether arrested progress, as Ecology; and so to carry it yet farther? All else, down to or up from utmost minutiæ of cell-structures, or subtlest biochemistry of protoplasmic change and results, is but the unravelment of the details of the Life-Drama which is increasingly opening before us, from minutest and simplest life to man's, and all in intimate interaction throughout, albeit with fascinating by-play too. In presence of this supreme world-spectacle, of which we are the awakening spectators, yet in which we are also taking our parts as actors in our time and turn, our doctrines of Evolution, our theories and philosophies of Life, are but reflective endeavours towards interpretations of its plot. The advances of each and all the sub-sciences of biology, be they small or great, thus return to their old source and there find fresh scope and significance: for, after all, "The play's the thing!" And if evidence be needed: Is it not plain throughout the essential life and search of the great biologists, from Aristotle to Darwin? And who, before Darwin or since, has been so characteristic and so productive a worker in and for Ecology, fully realised as Biodrama upon the vast world-stage of Inorganic Nature?

With all this insistence on the importance of Ecology, not only at the simple beginnings of biological studies, but as utilising their fullest development, much has still to be done towards a more systematised presentment of animal and plant ecology, before either can fully attract the more specialised and analytical workers in other fields. It is hard to convince taxonomists, anatomists, and histologists, embryologists and physiologists too; they are failing to recognise that Ecology has really got far beyond its simple anecdotic beginnings, often dubious at that. But ecologists, for the plant world, and for animals too, are increasingly utilising all special analyses of form and function and development for the individual life-histories they seek to elucidate, the biographies of species, and the association of groups, which they endeavour to write, and even map out with increasing clearness. All such inquiries are again but steps towards the main endeavour; nothing short of the panoramic visualising of the general drama of life as actually now in progress upon the world-stage; and behind this to realise its distinctive scenes in past geologic time.

The ecologist thus needs and seeks to know the stage on which the life-drama is being played, and has been played of old. He utilises all he can learn of present geography and distribution, and of that increasingly vivid reconstruction of past conditions and bygone forms of life which geologist and palæontologist are so admirably outlining; since his effort is to realize all organisms in their life at its completest, and thus see Nature as a concrete whole. Not merely therefore life as "the result and sum of organic functionings"; nor of these "as resisting death", and even this for the species, beyond the individual, nor even simply "the adjustment of

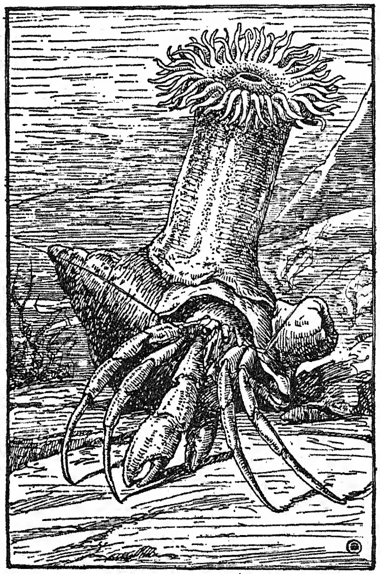


FIG. 13.
Commensalism between a Hermit Crab, Eupagurus, and several Sea-Anemones. From a specimen.

internal to external relations"; and so on: though each of these generalised statements is true. Ecology seeks to define more and more precisely how environment in general determines life, and particular environments particular lives; and beyond this fundamental setting of the scene, its main interest is with the reaction of organic lives to their environment, with their evolutionary advance, arrest or decline accordingly.

Ecological studies then fundamentally demand all we can learn of the environment of life; so here clear outlines, like those of Henderson for its physical and chemical conditioning and "fitness", are indispensable. After these we come to the physical geography

of sea and land, with meteorology and climatology, and all these from earliest times and conditions onward. The like, too, for bio-geography and palæontology, with the appearance of characteristic forms, so often with new ways of life, and their successful adaptation and widening distribution; yet often, too, their disappearance, for reasons we as yet mostly guess at, but which we would fain more clearly discern. Each great palæontologic scene has thus to be interpreted in time, and as an act of the life-drama preceding our contemporary one, in part no doubt detached from ours, yet in part also indispensably associated, and in ways we have to trace. One great principle is more and more clear; that with each great change of the geologic scene, with its manifold extinctions of forms often long dominant, new types have appeared to fill the places thus vacated, and often in strangely parallel ways of life, not only in the comparatively less changing sea and in inland waters, but in the air, and above all on land. Throughout all this has, of course, continued the elemental association of plant and animal life, and the dependence of the latter upon the former. Ever-increasing elaborations and intricacies of this widest adaptation have appeared, and similarly among both plants and animals. The conditions of our own human advent upon the life-stage, its ecologic conditioning throughout the past, and our ever-increasing human reaction upon living nature also (so largely destructive, yet not without selectively co-operative adaptation as well), thus fully bring us into the present scene, of the historic Eco-drama of Life in Evolution.

Concretely, then, as the modern movement of science becomes more comprehensively understood and applied in life and education, and as the fundamental sciences of the inorganic cosmos continue their intellectual progress and their practical applications, the present eclipse of "natural history" by them will not continue. As we are aided and strengthened by these preliminary studies and appliances, these will be more and more applied towards the better understanding of life in nature, and of its guidance in man. Scholar and student will know more of the inorganic world of heavens and earth, more of the mechanical, physical, and chemical sciences than ever, and of their arts as well; yet they will more and more utilise them all towards the essential studies of old described as "Natural and Civil History", and now as the sciences of life in evolution, organic and social. Are we asked, How dare we predict this?—the answer is open to all eyes. Our own lives are not only individual, but in intricate natural and human associations, and these in our respective regions of Nature. Our human homes and larger hives—be these village or town, city or metropolis—are still fundamentally regional; and our achievements are adaptations to nature's order in its evolution at best, or else disharmonies, and to its and our loss accordingly. Each region, each of its human groupings too, however

small each be in itself, has more than local interest; though this is fundamental to each, from infancy onwards. Each mind as it widens, each life as it enlarges, has before it the open secret of its actual and extending inter-relations throughout the wide world, cosmic, natural, and human alike; and these from the long past as well. What biology calls our ontogeny, and social life our education—each, of course, in its right sense of true and full development—is each essentially an adaptation to our region, to know it, and to be efficient in it. Yet for these apparently simple studies and activities no world-culture can be neglected, none of the arts of life ignored. Our whole world of life is made up of regions fundamentally like our own in cosmic conditions, from heavens to rocks and soil and waters, to sky and weather; and so for its plants and animals, its human life as well; so in our fundamental regional schooling we are being prepared and interested to know more and more of other regions of the surrounding world, and their past evolution. Without these, indeed, our own immediate region cannot be really understood; as, indeed, its schools and university, its libraries and Press so plainly exist to testify. Thus only can it now be efficiently worked and lived in; as the whole vast inter-organisation of human affairs shows, and even the daily details of our lives, from our food onwards. In short, as evolution comes into our philosophy of life, this becomes geographic, regional in the concrete: Ecology is thus comprehensively understood, and likewise participated in. Our younger generation, despite all their apparent fascination by mechanisms, or absorption in sports, are increasingly coming to all this. They are often turning to fuller nature-experience and appreciation, and towards varied occupational education and careers, and these truly ecological; i.e. consistent with the understanding and conservation of nature and life in evolution; and hence towards their own better development and survival accordingly.

The Environment and the Organism are the two great phenomenal interests arousing our observation; so we have tended (and only too readily, since so easily) to observe them apart. Thus geography on one side, and natural history on the other; and each with immediate and fascinating analyses of its own. While this separation lasts, each primarily concentrates on observing and recording the forms of his chosen set of phenomena; and with great results accordingly, the former in maps, atlas, and globe, and to geo-morphology, and the latter in its herbaria and museums, morphological also. In time the geographer has come to take note of plant and animal distribution and make its maps in his large way, as for forests and moors, plains and deserts; the zoologist and botanist have been stirred by the complemental interest, until they now add distribution maps even to the museum or botanic garden labels naming their species. This is enough for taxonomy and palæon-

tology; but not for Ecology, with its essential interests. These, of course, begin with recognising the way the life of its plants and animals is conditioned by their environment, in sea, lake or river, on land or in air, and by soil, climate and weather. But they soon pass on to the more intimate study of how particular groups and species, and among these their individuals and sexes and their offspring, even to animal societies and plant associations, interact with their environment in detail, and so search out the life-story of each and every living species; and this from its individual to its

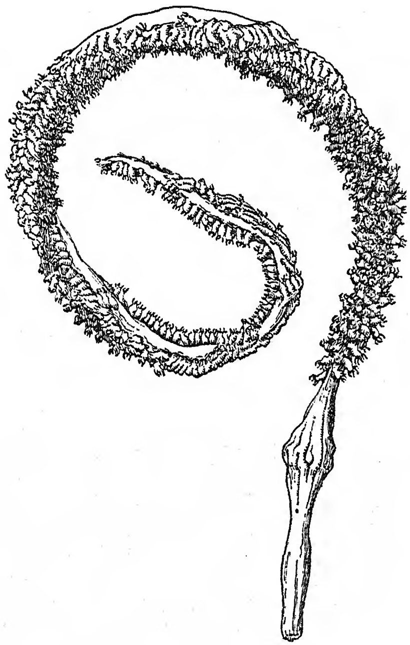


FIG. 14.

A Very Large Pennatulid Colony (*Anthoptilum thomsoni*), rising to a height of four feet above the ooze. From a specimen from off Japan. The sterile basal portion is fixed in the substratum; the upper part, bent round for convenience, bears numerous polyps, each about an inch long.

race and kin, with all their foes and friends. The ecologist is thus the untiring spectator of all the seasonal acts and daily scenes upon the geographic stage of Nature's Biodrama; and from the varied comedic and tragic parts acted by its innumerable players he discerns what he can of its general plot, even to its evolutionary development and significance. Thus, then, he links the older geography with the older biology, arousing each to fuller life, by marking out their reciprocal influence. And so much is already clear, that evolution

is no mere yielding of life to its environment, in simple self-adjustment so far as may be; life has been too much thus regarded, but that opens the way to passivity and degeneration. Fundamental though environment is, the progress of evolution is ever marked by active adaptation, with increasing domination of environment accordingly. Hence the progress, alike for individual and race, from encysted cell to highest forms of plant and animal life, and at length to man himself; indeed, even more and more for advance of nature's forms and their locations through his action.

In this book we are using the term "ecological" as more or less equivalent to the old-fashioned Natural History. Ecology is the study of the higher physiology of organisms, of organisms in the plural, and in their relations to other organisms and to their environments in space and in time. Digestion is a problem for the student of the physiology of the individual; parasitism leads to a consideration of host as well as parasite; the life of a beehive raises even more markedly ecological questions. Similarly, photosynthesis in the green leaf is a question for the physiology of the individual; in studying the root-tubercles of Leguminous plants, there are two parties to be considered; similarly the relation of flowers to their pollinating insect visitors is in the main a study for the ecologist.

ORGANISMS IN THEIR ENVIRONMENTS

(Haunts and Seasons)

In this chapter, illustrative of ecology, it is convenient to separate the organism-environment relation from the organism-organism relation. On the one hand, living creatures have entered into vital relations with their haunts and habitats, which have again in most cases to be thought of as changing throughout the year. On the other hand, living creatures have entered into vital relations with other organisms, including not only their kindred, within the family or the society, but entirely different types, whether parasites or partners or simply competitors. But the distinction between the two sections must not be pressed hard, since no rigid line can be drawn between an animate and an inanimate environment.

RELATIONS BETWEEN ORGANISM AND ENVIRONMENT.—There is a risk of looking too superficially at the fundamental facts of life. They require to be scrutinised, to use Fabre's favourite word. Everyone knows of the relation between organism and environment, but it is really a very complex set of relations which require analysis.

(1) There is the organism's relation of constant and normal dependence on its environment. For each kind of living creature

there is an indispensable minimum of supplies and influences (such as oxygen, water, food, warmth), apart from which it cannot develop, or grow, or continue to live.

(2) But environments are changeful and organisms must change with them; and in many cases there has come to be an established attunement between the living creature and the outside changes, such as the ebb and flow of the tide, the alternation of day and night, or the march of the seasons. There are ingrained or hereditary rhythms, which have become synchronous with external periodicities. The outside events serve rather as liberating stimuli than as direct causes.

(3) To particular changes in the environment the individual living creature often answers back—even a tree to a passing cloud, and an earthworm to the vibrations in the soil caused by the tread

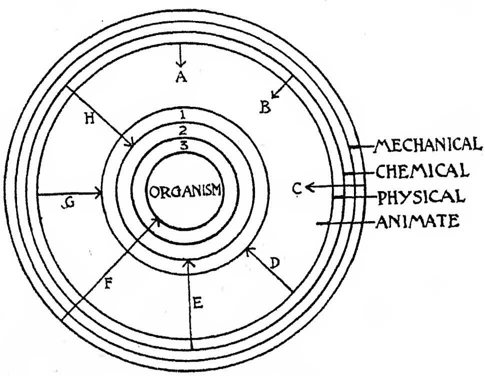


FIG. 15.

The Organism, with its three germinal layers (ectoderm, mesoderm, and endoderm) (1, 2, 3), is represented as surrounded by environmental influences—mechanical, chemical, physical, and animate—some of which penetrate further than others, as the various lettered arrows suggest.

of many feet. These are immediate responses or reactions, and sometimes they are worthy of being called *adjustments*, as when the warm-blooded bird or mammal on a very cold day automatically regulates its production of heat to compensate for its unusual loss. Even subtler is the way in which animals with a power of rapid colour-change, e.g. flat-fishes, adjust their coloration to suit the gravel or sand on which they are resting, thus sometimes securing protection by unconsciously making themselves invisible.

(4) When some peculiarity in the environment impresses a lasting change on the organism, that is called a modification. The indent or imprint transcends the limits of organic elasticity and persists after the inducing causes have ceased to operate. As examples may be mentioned: Sun-burning in the course of a long holiday, or thicken-

ing of fleece after transport to a cold country, or the gradual blinding of goldfishes in a dark room. Sometimes the modification lasts for the rest of life; sometimes it is gradually lost. Modifications take a firmer grip than do transient adjustments, but some do not last a lifetime as others do.

(5) In many cases there is reason to believe that the environment affects the organism for better or for worse, although there is nothing to show for it. We mean that it may affect the germ-cells without *appreciably* affecting the body or soma. This is indicated by many experiments. Some of these show that the general vigour of the germ-cells may be improved or depreciated; and in experimental conditions it may be that the environment, e.g. through radium rays, kills the germ-cells. On the other hand, ultra-violet rays may improve the whole vigour of the organism, germ-cells included. Where viviparity occurs, and especially in cases of ante-

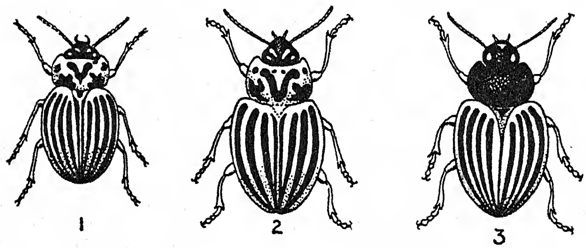


FIG. 16.

Variations in. Potato Beetle (*Leptinotarsa decemlineata*). After Tower. The three forms (1–3) differ in the details of their marking.

natal symbiosis, as in placental mammals, the vigour of the offspring may be increased or decreased by the quality of the surroundings.

(6) By themselves we are inclined to place those cases where a change in the environment of the parent provokes a variation in the offspring, through some disturbance in the germ-cells. Thus Tower subjected potato-beetles (Leptinotarsa) to unusual conditions of temperature, pressure, and humidity, when the male or female reproductive organs were at a certain stage of development. The body of the parents showed no modification, but there were in some cases remarkable changes in the offspring, in colour and markings, and even in minute details of structure. There was no reversion in the offspring of these variants. Here the environment acted as a stimulus to variability, and it is likely enough that this often occurs in Nature. But a repetition of Tower's important experiments is urgently needed.

(7) Quite different from the preceding relations is the selective

or eliminative action of the environment. Organisms compete with one another—the most familiar form of the struggle for existence—but as Darwin insisted, the struggle includes the relations between organisms and the inanimate environment. As he said, the plant is struggling at the edge of the desert, but not necessarily with any other plants. The struggle for existence includes all the answers-back that living creatures make to environing difficulties and limitations, and in an automatic way the environment is a sieve as well as a stimulus. Its sifting is often discriminate, and this makes for the establishment or improvement of adaptations.

But we must not think of Nature's sifting too fatalistically, as

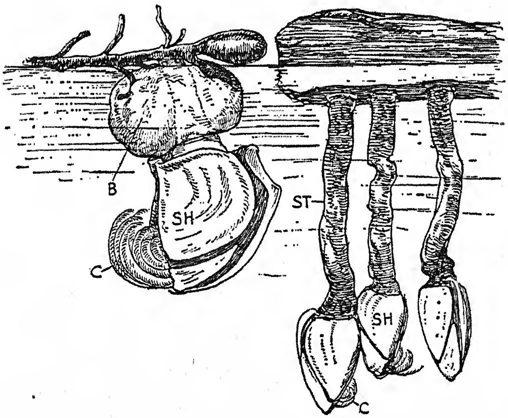


FIG. 17.

Adaptation in a Barnacle. To the left three common Ship Barnacles (*Lepas anatina*) attached to a piece of floating timber. From a specimen. The animal proper, at the end of the long stalk (ST), often six inches in length, is encased in its substantial 5-valved shell (SH), and protrudes five pairs of biramose thoracic limbs (C) (the cirri of the Cirripede), by which it wafts microscopic food into its mouth. The other species, the floating barnacle (*Lepas fascicularis*), attaches itself to floating seaweed or the like, and obviates the danger of dragging this down, beyond the surface zone of nutritive abundance, by secreting a buoy (B).

if organisms were always like helpless fishes, around which the environmental net closes, only the little ones escaping through the meshes. On the contrary, in varying degrees living creatures are agents; they thrust as well as parry; they act on their surroundings, modifying them; they are ever seeking out new environments and conquering them.

Thus, without going farther, we see that the range of relations between the living creature and its surroundings is complex, including:

(1) functional dependence,
(2) periodic attunement,
(3) reactions and adjustments,
(4) lasting modifications,
(5) influencing the vigour of the germ-cells,
(6) provoking variations in the germ-cells,
(7) bringing about sifting and again initiative.

We have given a more detailed analysis in *Evolution* (Home University Library), 1911.

THE MARCH OF THE SEASONS

One of the largest facts of life is its waxing and waning as the earth moves round the sun. This is the subject of the science of Phenology—an inquiry that comes home to us in temperate countries, where the seasons are clearly punctuated, and do in no small measure hold living creatures in their grip.

As the sun is the source of almost all the energies of the earth, our income—of heat and light in particular—varies with our seasonal position in regard to the centre of our system. The basal fact is that the ratio of the heat supply in summer to that in winter is 63 : 37 in our latitudes.

Beginning with spring, we see it as the season of renewed activity and strength. The water in the soil begins to move again, and there is a quickening of the cycle of mist and cloud and rain. Into the quiescent seeds the water begins to soak, sharing in the fermenting that is going on; the seeds sprout, the seedlings lift their heads above ground, the brown earth becomes green. The water rises to the tops of the tall trees, and the buds that were formed in the warmth of last summer's sunshine begin to grow and swell and open, scattering the protective bud-scales on the ground. Almost everywhere over the earth there is stretched the green veil which enables the plants to capture part of the power of the sunshine. Spring is a time of fresh life, of reinvigoration, of becoming young again.

The "winter-sleepers," like hedgehog and dormouse, come out of their retreats, with a new lease of life after their long rest. Spring is a time of reawakening. The migratory birds, like swallow and swift, cuckoo and nightingale, begin to return from their winter quarters in the south, and some of them are no sooner here than they begin to sing songs of love. For spring is a time of love-making. Naturally enough it is also a time of young things, for eggs are laid and new creatures are born. Who can think of spring without picturing caterpillars and tadpoles, nestlings and lambs? The ponds

and the shore pools, which seemed so empty in winter, begin to teem with what we may with Charles Kingsley call "water-babies", which form the basal food supply for aquatic animals, just as the multiplication of the blades of grass, in the wide sense, is the most important event on land. The circulation of matter from one embodiment to another is slowed down in the winter, but it is quickened again in spring. Grass begins again to become flesh, and one reincarnation follows another all the world over.

Summer means a great increase of income and therefore the possibility of a great increase in expenditure. The day is longer and warmer, and what may be called the industry of green plants is incalculably great. Every sunlit green leaf is making carbohydrates and proteins, and great quantities begin to be laid past in root-stock and tuber, corm and bulb, to give the plant capital for next spring. But as leafing is characteristic of spring, so is flowering of summer. No doubt there are many beautiful spring flowers, mostly white and yellow, like snowdrops and celandine, but it is in summer that the crowded floral pageant begins to move, and its colours seem to heighten as the months pass. It is in summer that we see so much of the most important linkage in the world, that between flowers and their insect visitors. "Most important" because many of these visitors, notably the bees that come for nectar and pollen, carry the fertilising golden dust from one blossom to another blossom of the same kind. It is this fertilising pollen that makes the possible seeds or ovules into real seeds that will sprout; in other words, a male nucleus from the down-growing pollen-tube fertilises the egg-cell within the ovule within the ovary of the flower. Summer is characterised by industry. In spring, both among plants and animals, there is much living on the strength of the past; in summer there is living on the present for the present, and for the future. What studies in animal industry we see in the summer months! Just as in mankind, there are hunters and fishers; there are miners like moles and foresters like beavers; there are agricultural ants and others that keep domestic animals. The climax of summer industry is to be seen in the ant-hill, the termitary, and the beehive.

Autumn marks the turn of the tide that began to flow in spring and reached high-water mark in summer. The days become shorter and colder. Spring for foliage, summer for flowers, autumn for fruiting; and the meaning of the fruit is to secure the dispersal of the seeds—the sowing of the next generation. In some cases the nectaries of the flowers close and the surplus sugar is drafted into the fruits, making them tempting to birds. It may seem a bad beginning to be swallowed by a bird, but the seeds are in such cases usually very hard and pass down the bird's food-canal not a bit the worse. Other fruits like those of jack-run-the-hedge and burdock catch on to passing animals and get rubbed off far away. Others,

again, like thistle-down and dandelion-down, are minute nutlets with a parachute of silken hairs which the wind wafts hither and thither till some of them, at least, are caught on suitable places.

Very characteristic of autumn is the withering and fall of the leaves. They have worked hard all the summer, but they would be sources of weakness in winter, when soil-water is less available and when freezing of delicate tissues is apt to occur. So the leaves, transfigured in dying, are shed in the autumn, which is often appropriately called "the fall". It is interesting to find that before they are separated off by a partition which heals the wound they surrender to the stem almost all that is worth having. The fallen leaves which the earthworms bury contain little more than dead tissue and waste products.

What the trees do in surrendering vulnerable parts is also seen among animals. Thus many of the plant-like zoophytes in the shore-pools "die down" in the autumn, reminding one of herbaceous plants. The green fresh-water sponge dies away in autumn, all but little pinhead clusters of cells called gemmules, which eventually float away from the dead skeleton and start new sponges in spring. The sacrifice of parts or members finds expression in some of the social insects in a striking way, for of the wasp colony and the humble-bee family only the young queens are left to face the winter. In the beehive there is an eerie cold-shouldering and final killing of the drones in autumn. No doubt autumn must be thought of as a time of retrenchment!

Characteristic of the season and symptomatic are the "flights" of small gossamer spiders, a passive migration on the wings of the wind; and another note is struck in the industry of earthworms, which are now at their busiest in taking withered leaves underground.

Winter is a difficult time for many plants and animals in North Temperate countries. It is a yearly reminiscence of the Ice Ages which have occurred repeatedly in the history of the earth and have from time to time severely pruned the growth of life. Short days, low temperature, stormy weather, scarcity of food—these are sharp pruning-hooks of winter. The problem is to keep alive, and there are many solutions. Neatest of all is the migration solution, for the birds that come as summer visitors to North Temperate countries take their departure in late summer or autumn for more genial climes. Thus, they know no winter in their year; they have not only annihilated distance, they have circumvented the seasons. Very different is the hibernation-solution exhibited by some imperfectly warm-blooded mammals, like the bats, which seek out secluded nooks where the temperature keeps above that outside, and sink into a strange almost reptile-like state. Out of their weakness in being imperfectly warm-blooded, they have made a strength,

for hibernating works well. In many lower animals the solution is suspended animation or lethargy, and there are many other ways of meeting the winter—by storing, by blanching, by putting on more fat and fur, and so forth. There is much sifting, no doubt, but winter must be thought of in the main as a resting-time in preparation for another spring.

IN ILLUSTRATION OF SEASONAL ECOLOGY: SHOWERS OF GOSSAMER

On fine days in autumn, when there is a light breeze, we often feel the touch of a gossamer thread across our face as we walk. The sun sometimes illumines the threads as they float in the air, and when they sink on to the ploughed fields or the golf-links they form a vibrating veil. If we kneel down and look against the light we sometimes detect a slight iridescence. These fallen threads must be distinguished, of course, from the horizontal webs which some kinds of spiders weave close to the ground, for the gossamer consists of long filaments which are not viscid and have no arrangement at all. At the ebb-tide of the year, but before all the insects have disappeared, it rewards one to look for the ground-webs, often decorated with dewdrops and hoar-frost crystals. Many of those made by "money-spiders" are about the size of shillings or florins. They recall Stevenson's description: "And every fairy cob and web, with drops of dew bediamonded."

The floating gossamer that we catch on our face or on our clothes often consists of single threads, but there may be two or four. If we are lucky we may intercept the little aeronaut itself, hanging back downwards from a tiny hammock of silk from which threads float out, often in two directions. This hammock is the spinner's magic carpet on which it makes wonderful journeys, sometimes for fifty miles. In Canada we caught some of these silken balloons about the size of black currants, and provided with very long threads. Why do they float? As Jonathan Edwards pointed out in 1716, when he was twelve years old, the resistance of the air to the large surface of the silk threads serves to counteract the down-pull of gravity. They float like dandelion-down.

The essentials of the gossamer story were discovered in 1716 by that remarkable boy, who afterwards wrote a famous book, *The Freedom of the Will*; but we are always seeing a little farther into it, and in this connection it is a great pleasure to refer to Savory's scholarly *Biology of Spiders*. Small spiders of various kinds climb up on gateposts, palings, and tall herbs. In so doing they obey an inborn predisposition or tropism to move, when they are young, away from the ground. We may call it a "negative geotropism" if we

like. Fabre tells how a family of spiderlings hatched out at the foot of a high pole proceeded to climb up and up, day after day, till they reached a very absurd height. No doubt the young spiders are experiencing an autumnal restlessness, but we may be sure that they do not climb up to a vantage-point because they argue that they will thus get a better send-off. They are obeying what is, nowadays at least, a racially enregistered tropism to climb against gravity.

The spiders dispose themselves with their head towards the slight breeze, and it is interesting that the thread-spinning instinct will not become active unless there is a current in the air. Blackwall showed long ago that spiders imprisoned on a flower-pot in a room would not begin to parachute until a slight draught was produced by opening a window. Some air-current is needed as the instinct-liberating stimulus.

The spider pays out a thread of silk, or there may be as many as four. In any case, though we say "as thin as gossamer", each thread is a multiple jet of liquid silk, hardening instantaneously on exposure to air. When the wind begins to tug, the spider lets go with all its eight legs at once and, usually turning upside down at the same moment, is borne on the wings of the wind to an unknown goal. Careful observers assure us that it can add to the length of the ballooning threads if the wind falls; and it can furl its sail if the wind rises. Sooner or later it begins to coil in the threads, and thus it sinks to earth, perhaps many miles from the starting-place. When tens of thousands of spiders do this on a fine autumn day, there may be an extraordinary shower of gossamer covering acres of links and lea. Many of the threads we see floating in the air have no spider attached; these may be broken-off failures or they may be threads that have served their purpose.

It takes an appreciable time to write the words climbing, posing, spinning, vaulting, parachuting, but the process often takes place with great rapidity. Almost before we could say "gossamer" we have seen a small spider run along our finger and set sail from the tip. It is an instinctive performance, requiring no individual apprenticeship. Two other notes may be useful. First, there is no particular kind of gossamer-spider, for the habit is exhibited by many young small spiders belonging to light-loving species. Secondly, gossamer is by no means restricted to autumn, its conspicuousness at that time of year being due to the fact that spiderlings are then most numerous and most crowded.

For there is no doubt that the ballooning is a method of passive dispersal, which enables the spiders to get away from places that are overcrowded or overdry, or very scantily frequented by the insects on which spiders depend for food. There is no doubt that this neat device of flying without wings sometimes spells disaster, for

the aeronauts cannot direct their course and may be blown out to sea. Thus Darwin records that when the *Beagle* was sixty miles from land the rigging was covered one day with a multitude of little spiders! We cannot expect these subtle adaptations to meet all contingencies; and even the apparent fatality of being blown far away may lead, and indeed has led, to the peopling of high mountain-plateaus and distant islands of the sea.

When we think of long aerial journeys made by flightless animals, made on the whole successfully, made with some measure of plasticity, and more or less perfect on the first trial, we cannot but ask how such a device could arise at all. As Goethe said: Animals are always attempting the next to the impossible and achieving it; and of this there is no better instance than the flight of gossamer-spiders. By what inspiration did it begin? The general answer is not very remote; the device is an outcome of the drag-line habit. For it is almost a universal habit of spiders to pay out a drag-line of silk when they are in any difficult or critical situation. A spider is creeping back-downwards along the roof of our room, holding on by its toothed claws to the roughnesses of the whitewash. If a flake should give way under the tips of its toes the spider has time to touch an intact spot with its posterior spinnerets. The exuded silk adheres, a rope is instantaneously paid out, and down this the spinner descends with dignity. There is a touch of perfection in the way it sometimes changes its mind, so to speak, when half-way down, and proceeds to climb up its own rope, which disappears as it climbs. This is finer than the Indian rope-trick, and it actually occurs.

Now it is from the drag-line habit, as Savory well shows, that webs began, and the comfortable lining of the nest, the cocoon for the hidden eggs, and the threads that make the silken parachutes on which the spiders are buoyed through the air. Nowadays the performance is instinctive, but it is quite reasonable to suppose that each fresh inspiration was tested from age to age by individual intelligence. Animals *play for themselves*, for better and for worse, the hands of cards which they inherit; and evolution is thus neither magical nor fortuitous.

ENCYSTATIONS.—Among the simplest organisms there are many instances of encystation in face, not only of winter, but of other difficulties. Thus the Amœbæ may encyst in conditions of drought, and it may be that the reduction of locomotor activity and the secretion of a cyst can be interpreted as direct reactions to the scarcity of water. The protection may be afforded almost automatically. In the same group may be ranked the formation of special "winter-eggs" in some small crustaceans, such as Daphnids. They differ from "summer-eggs" in their more resistent shell and

larger amount of yolk, in requiring to be fertilised, and in their slower development. They are adaptively protected, not only against cold—for they can survive the freezing of the water—but against drought, and their formation is by no means confined to the winter. It might be better to call them "resting-eggs" (German, *Dauer-eier*).

In the Turbellarian Mesostoma there are hard-shelled cross-fertilised "winter-eggs" and thin-shelled summer-eggs, probably self-fertilised within the hermaphrodite parents. The winter-eggs are laid in summer, but remain dormant through the autumn and winter. Some species of Mesostoma form only the hard-shelled ova, and this is true of most of the members of their family—the Rhabdocœl *Turbellarians*, a fact which may account for their wide geographical distribution, since such well-protected eggs can travel on birds' feet, etc., more safely.

Reproduction in Rotifers is somewhat complicated; but we may distinguish (*a*) the ordinary "summer-eggs" which are unfertilised and develop quickly; (*b*) in certain conditions, e.g. the approach to a temperature associated with the drying up of the pool, the production of small, unfertilised eggs which develop into males; and (*c*) the formation of fertilised "winter-eggs", with hard and often prickly shells. These are particularly adapted to withstand drought, and are best called "resting-eggs". In their development there is an interesting adaptive suppression of a larval phase that is commonly seen in the case of the "summer-eggs".

A comparison is often made between the lethargic condition of animals and the state of the sown seed in the ground. But it should be noticed that the latent period in seeds is a time of necessary preparation, and may extend over more than one winter. In the corn of wheat that "dies" in the ground there are intricate processes that prepare the way for the development of the seedling. Who shall say whether there is in the grain, as Treviranus thought, a dim dreaming of the ear that is to be, but there is no doubt as to the fermentations and cell-divisions that are involved in germination. The "dying" is a being born, and the seeming inactivity a restlessness. It is plain that this should be compared only to the reawakening phase in the inert snail or in the dormant chrysalis. The dry seeds in the store, alive yet not living, they are what we should compare with those profound winter sleepers in which functionality of every sort is reduced to a minimum.

OTHER STATES OF VITA MINIMA.—From among the lower orders of animals a good example of the lethargic state, where vitality sinks to a very low ebb, may be found in the Roman snail. Getting under moss or the like in some sheltered place, it makes a smoothly lined hole in the ground, and goes to rest with the mouth of the shell upwards. Retracting the whole of its body, it draws across

the opening of the shell a fold of skin, which secretes a lid first of rapidly hardening mucus and then of lime, layer after layer of carbonate and phosphate. This forms the tightly fitted winter-lid or epiphragm, which is perforated by a minute hole permitting interchange of gases. After the snail has finished the calcareous lid, it draws itself still farther back into the shell, and makes another door, quite membranous, and then another and another. There are sometimes six, all with empty spaces between them. Then the creature sinks into a strange dead-alive state for nearly six months. The heart beats twice or thrice a minute instead of the fifty times observed in summer; the respiration is slow diffusion; the glycogen or animal starch stored by the liver is used up; some of the tissues seem to be in a bad way. There are many interesting points: that the snail begins to make the lid at the proper time even when it is kept warm, that it can be kept asleep in continuous dry cold for twenty months, that if it is wakened artificially in gradually warmed water it soon falls asleep again when it cools. Meisenheimer records the interesting fact that snails with broken epiphragms always die when subjected to a temperature of —100 deg. C., while those with intact epiphragms can survive a day or more of that terrible cold. In normal cases the Roman snails become restless in April, and burst their prison-doors with violence.

Some fishes of the carp and eel tribes burrow into the mud at very low temperatures (5 deg. C.) and become extremely lethargic. The heart-beats may fall from 20 or 30 to one or two per minute, and the weight decreases as the fat and other reserves are consumed. A carp will sometimes survive being frozen within a block of ice, but not, of course, if the blood freezes. In all cases rapid thawing is fatal, and it may well be that the pure water produced within the tissues during thawing is destructive to the protoplasm. Amphibians also exhibit this winter lethargy, the frogs, for instance, betaking themselves to the mud of the pond, where they lie buried, not asleep in any exact sense, but with mouth shut, nostrils shut, eyes shut, breathing through the skin, and with the heart beating feebly. On the Continent salamanders are sometimes found wintering together in large numbers.

As to reptiles, some careful observations have been made on lizards. Two or more lie together, motionless, but not rigid, with closed eyes and no perceptible breathing, but sometimes with open mouth. They keep the vital fire burning by consuming two fatty bodies which lie near the hip girdle. It is interesting to learn on good authority that our Scottish viviparous lizard sleeps for nine months of the year at Archangel. A large number of slow-worms are sometimes found huddled together in their winter retreats. The Greek tortoise normally buries itself in the ground when winter sets in, and lets the current of its life run slowly. One remembers how Gilbert

White's tortoise, that he wrote about so often, used to dig out a hibernaculum in the garden, and actually survived fifty-four British winters.

TRUE HIBERNATION.—Turning to mammals, among which we find the true hibernators, we at once find a clue put into our hand in the fact that the capacity for winter sleep has a curiously irregular distribution. The mole is not very far removed zoologically from the hedgehog, and both are largely insectivorous. Why does it not hibernate as the hedgehog does? The probable answer is that the mole, being a burrower, can get below the frost's grip, and thus does not need to hibernate. Water-shrews do not hibernate, while bats do; and the probable reason is that while flying insects are far to seek in winter, there are many aquatic insects and pupæ to be found by looking for them. Similarly, it is not difficult to find plausible reasons why true squirrels, rabbits, hares, lemmings, water-voles, porcupines, beavers, ermine, foxes do not hibernate, while ground squirrels, true marmots, dormice, Canadian jumping mice, racoons, skunks and spiny ant-eaters do. It seems that the capacity for winter sleep has arisen as an adaptation in the course of natural selection, and is not a necessity imposed by cold and scarcity on certain kinds of constitution. We are not aware of any *a priori* reason why birds should not hibernate; they evade the winter by migration, and in all probability have never given winter sleep a trial. It should also be noted that polar mammals do not hibernate, for the hibernation of a warm-blooded animal ends fatally if there is very prolonged exposure to very low temperature. The polar mammals meet the winter by thick fur, by stores of fat, by migrating, and so on, but not by hibernation. It is true that the mother polar bear lets herself be snowed up (all but a ventilating hole), and gives birth to her cubs (in January) in this retreat, but there is no true hibernation of the type which the hedgehog and hamster illustrate.

There is, as one would expect, considerable diversity in the duration and the depth of the winter sleep. Marmots and bats often hibernate for six months, dormice and hedgehogs for three. Bats are occasionally seen flying in winter in Britain, but they tend to sleep uninterruptedly; marmots may waken up five to ten times in the winter, and go to sleep again. The hedgehog is probably more penetratingly affected by its hibernation than any other mammal. On the whole, it may be said that the true hibernation of some of the warm-blooded mammals is a much deeper change than the lethargy of the cold-blooded reptiles and the like. Lizards are often reawakened by a very sunny day in mid-winter, and everyone is familiar with insects which awaken unseasonably and to their own destruction.

What are the significant facts in regard to the state of the body during hibernation? One of them, well worked out by Prof. E. W. Carlier of Birmingham, is that the constitutional change is very thoroughgoing, like a disease indeed. There are subtle alterations in the inmost recesses of the body, and not all on the minus side, for the irritability of some of the muscles is markedly increased. Another general feature is the all-round reduction of the metabolism; the wheels of life are slowed; expenditure is at a minimum; the fire is hardly burning. There is little or no respiration, as is shown by the beautifully exact measurements which Weinland and Riehl and other physiologists have made of the minute output of carbonic acid gas. A correlated fact is the lowering of the temperature towards that of the surroundings, for there is no attempt made to keep up the characteristic mammalian warm-bloodedness. It is not so much, we think, that the heat-regulating arrangements break down, as they do in the opposite extreme of fever; it is rather that they are given up when hibernation is signalled. In any case, the temperature sinks till it may be only 1° C. above that outside of the body (as in the spiny ant-eater and some bats). It should be remembered that the temperature of cold-blooded animals is normally just a little above that of their surroundings (1° or so in fishes, 4° or so in amphibians, 4° to 8° in reptiles). Pembrey and Hale found hibernating dormice with a temperature of 9° to 14·5° C., instead of a normal of 31° to 36° C., and Marès found bats in a grotto at Maestricht with a temperature of 7° to 7·2° C., when the external temperature was 6·4° to 7·7° C. It is very interesting to find that many of the hibernators have in the summer a variability of body temperature greater than is usual among mammals. A fourth general feature is of a different order, that the hibernating capacity is associated with a tendency to deposit fat, not only in the usual place beneath the skin, but elsewhere—e.g. on the walls of the chest, even pressing the lungs dorsally, in the arm-pit, and at the loins. It was long since recognised that the so-called "hibernating gland" is no gland at all, but a reserve of fatty tissue traversed by blood-vessels. It is plain that winter sleeping could not have been successful had it not been associated with laying up a store of fat, the slow combustion of which ensures the necessary minimum of animal heat. Captive hibernators, which have not been able, for some reason or other, to accumulate fat, will not go to sleep. On the other hand, it has been noticed that super-fatted individuals tend to go to sleep too soon, as readers of the *Pickwick Papers* will remember.

The problem of the origin of hibernation remains obscure, and we have sympathy with Horvath, one of the notable investigators of the subject, who said: "In the first place, it is not sleep, and, in the second place, it has nothing to do with winter." In truth, the hibernating state has very little resemblance to normal sleep, and

it is an adaptation to meet bad times, especially scarcity of food, not necessarily winter. Horvath got one of his sousliks (pouched ground squirrels) to hibernate as early as August. When we think of the bats going to sleep when the insects disappear, and reawakening when the insects are ready, it seems the best of possible worlds. But how did this beautifully adaptive punctuation arise? Were there wise bats long ago who bent their heads before the approaching storm, and, escaping, transmitted their wisdom? Is there a tradition among bats, as among the peasants of Klosk, that it is a fit and proper thing to go to sleep when the wind is very cold and the sun's rays are very low? Or has there been gradually coerced upon the bat's constitution a rhythmic tendency to sleep when winter approaches? Or is it not rather that the living creature is inherently an experimenter, whether in its explicit form as adult, or in its implicit form as germ-cell, restlessly trying this and trying that if so be that it may better itself? Or an artist, rather, in an organically instinctive way, suggesting this and suggesting that, if so be that it may achieve a greater harmony? Less metaphorically, perhaps, it may be that the capacity for hibernation arose as a germinal variation—expressing itself in the heat-regulating centres that probably have been established in the brain of warm-blooded animals—a variation that consisted in great part in lowering the body-temperature and in a consequent depression of vitality. All unconsciously, the pioneer winter-sleeper met the difficulties looming ahead by a variation in the heat-regulating arrangements, anticipating the cold by becoming cold. This implied immobility, slow breathing, slow circulation, reduction of excretion, and so on. It is not inconsistent with this theory to suppose that there may be some lowering of the blood-pressure through the retention of waste, or some auto-intoxication of the system, as Errera insists; or that the cold of winter or scarcity of food may serve as the stimuli which touch the spring of the hereditary predisposition and set it a-working at the proper time. In any case, winter sleep is very interesting as an illustration of Nature's tactics. It is a successful case of stooping to conquer—a relapse from activity to passivity, from agency to inhibition. The animal becomes almost like a plant, "lying low and saying nothing," as Brer Rabbit put it, and in due time it reawakens refreshed. The warm-blooded bats and hedgehogs, dormice and marmots, sink back towards the level of their cold-blooded ancestry among the reptiles. It is a dangerous game, and it is probable that many have tried to play it with fatal results to themselves; but when it has been successfully learned it is notably effective and one of the finest instances of life's resourcefulness.

We have laid emphasis on the difference between hibernation and ordinary sleep, yet, after all, and with every due distinction and precaution taken against confusion, is there not something in

the old popular notion of all these varied phenomena in terms of sleep—say, rather, as evolving from some of its deeper phases, and with their longer periods of seasonal operation to dwell in? Or at least, have not these seasonal phenomena, and the ordinary nightly one (or ones) of sleep, some traceable development from that relatively passive state which follows the cessation of ordinary daily activities as far as may be, consistent with the maintenance of the more or less slowed-down machinery of life (*see* physiological section on Sleep).

It is difficult to discover the most natural arrangement for the various phases of reduced vitality which we have illustrated; and in any case they must not be thought of in linear order, since they are *analogous* adaptations to difficult conditions, and have probably arisen many times independently in different phyla.

Perhaps it would be clearer to separate off the cases of dormant eggs (and even seeds) since these are *reproductive* adaptations and not adult individual ones.

It may also be clearer to separate off the encystment of Protozoa, since this must be thought of in connection with their unique power of evading natural death. Yet it is certain that in some adult multicellular organisms there are processes of rejuvenescence during the long rest of a dormant or encysted phase.

The difficulty of natural arrangement is further illustrated by cases like chrysalids, where the quiescent pupa undergoes an histolytic de-differentiation (in varied degrees of intensity) and is built up on the new architectural plan of the adult insect. The pupation may have been a seasonal adaptation to begin with, but in many insects it may be evaded for several winters, while, on the other hand, there may be successive pupations in two or more summer generations. When the histolysis or tissue-dissolving of the larval organs and tissues is very thoroughgoing, as in most Dipterous Flies, there must be very intense metabolism in the "imaginal folds" or discs of rejuvenescent cells which form the foci of the resumed development. The following scheme is suggested:

I. Arrest of Vital Processes, sinking down to lethargy, yet without adaptive structural change, as in dried-up Nematodes, Rotifers, and Crustaceans.

II. Encystment, when there is a protective investment, as in the winter snails, many Protozoa, seeds, etc.

III. Lethargic Torpor, when the everyday functions approach a standstill, as in frogs and reptiles in their winter retreats.

IV. Comatose condition in those mammals, such as badger and bear, which do not hibernate (in the strict physiological sense), but are often very sleepy and may doze for days. This is nearest normal sleep.

V. Hibernation, as in hedgehog, dormouse, marmot, and some bats, where there are profound changes in the metabolism of the body, and a relapse from the characteristic mammalian warm-bloodedness. Here should be included the similar state of æstivation, which occurs as a reaction to extreme heat.

VI. By themselves, and probably to be regarded as regularised pathological conditions are the de-differentiations of some Polyzoa and Tunicates, where the body or part of it undergoes collapse and passes into a resting stage with much simplified structure, from which, when prosperous conditions return, there may be an emergence of a rejuvenated and reconstructed organism with a new lease of life.

IN ILLUSTRATION: FROZEN PLANTS.—Living matter usually contains about 70 per cent. of water, and there can be no understanding of vital processes without recognising the rôle of water. On the other hand, in times of prolonged frost we cannot but think of the danger that organisms run in having so much water in their composition. Why does this water not freeze? and if it freezes will this not mean death? In many places there is often lasting frost such as Shelley pictured:

> A winter such as when birds die
> In the deep forests, and the fishes lie
> Stiffened in the translucent ice, which makes
> Even the mud and slime of the warm lakes
> A wrinkled clod, as hard as brick.

Our question is how the plants get on during a prolonged, severe frost. We do not refer to those that die down so that they are wholly protected by the earth, and it may be a blanket of snow; nor to those that are specially protected by thick epidermis, or by wool, or by resinous bud-scales, or by bark, and so on; we are thinking of ordinary plants like daisies and groundsel, and the glossy ivy, and the grass. How do they survive when the temperature falls below zero? What charm have they that many imported garden plants have not?

Those who grow plants in an unheated greenhouse are familiar with the wilting of some kinds of leaves in very cold weather. Experiments show that this is because the leaves are continuing to give off water vapour while the roots in the cold earth are unable to absorb enough to make good the loss. Thus the leaves sink down wilted and may eventually die, though there is no actual freezing.

But Prof. Molisch has shown that in cases where the loss of water and warmth from the leaves is checked by using a bell-jar or by some other device, there may be a dying away, although the

temperature does not quite reach the freezing-point. The leaves become discoloured and die. It seems that the chemical routine or metabolism may be fatally disturbed although there is no actual freezing. Much depends on the length of the exposure.

It is possible to surround the stage and lower parts of a microscope with a freezing mixture, so that the process of congealing can be intimately studied, and this has been done in great detail by Prof. Molisch. Living matter is a colloid, that is to say, a fluid in which there are suspended or dispersed innumerable ultra-microscopic particles and unmixing droplets, presenting an immense superficial area if all their minute surfaces could be added together. In a very fluid colloid or "sol" the suspended particles or droplets are in a state of quivering "Brownian movement", for they are being bombarded by the freely moving molecules of the medium in which they are suspended. But this readily passes into a "gel" state where the particles become "set" in a network or the like which imprisons little vesicles of the fluid medium. We have already referred to the fundamental fact that living matter or protoplasm is in a colloidal state, and many a living cell can readily pass from "sol" to "gel" and back again.

But when such a colloid as the milky juice of the indiarubber-tree is frozen, the droplets of rubber rush together to form a network and ice-crystals form in the meshes. As the crystals go on growing they necessarily fix more and more of the water, and this is the sort of thing that happens when a living cell freezes. Molisch has shown (1) that the ice may be formed inside the cell-substance, as happened when he froze an Amœba or the stamen-hairs of Tradescantia; or (2) that it may form a wall around the outer surface of the cell, as in the case of the common green threads called Spirogyra; or (3) that there may be a combination of these two processes. But in all cases there is a withdrawal of water to form ice and a consequent shrivelling of the protoplasm. In the majority of vegetable tissues the ice is formed outside the cells, and this is less likely to be fatal than when it is formed in the very heart of life. Whether the formation of ice is fatal or not depends on various factors, finally perhaps on the specific structure of the living matter of the plant. In many cases, such as daisy and conifer, the tissues may be frozen hard without losing their power of recovery; in other cases, such as potato tubers, tobacco plants, and the leaves of the vine, the internal formation of ice is always fatal.

As we have already hinted, there are many ways in which plants may circumvent the intensity of the frost. There are external protections, such as hairs and bark; there is a sacrifice of vulnerable parts, such as leaves; there is the assumption of a very dry state with water-content at a minimum, as in seeds. Moreover, cell-sap may not freeze as easily as pure water, and the minuteness of the capillary

spaces in the plant's cellular architecture will lower the actual freezing-point.

But suppose the plant does freeze, what is it that kills? The old answer, that there is bursting and tearing of tissues, does not seem to be generally true. The widespread belief that it is the thawing, not the freezing, that kills is not warranted except in a few cases. There is more to be said for the view that it is the withdrawal of water to form ice-crystals that is fundamentally fatal. It may fatally damage the molecular architecture and bring about chemical disintegration; or it may make the cell-sap so concentrated that it becomes poisonous; or it may be that different plants have different temperature minima for their metabolism and that when they stop for a long time they cannot begin again. But in any case there is notable individuality, for one kind of plant dies before the freezing-point is reached, while another can survive being frozen stiff for weeks or even months.

RHYTHM IN LIFE

A torrential stream gives one a vivid impression of continuity, but the waves of the incoming tide illustrate rhythm. Using the word widely, we mean by rhythm the regular recurrence of certain changes or events, but there are very simple rhythms like day and night which hardly deserve to be called more than alternations, and there are complicated rhythms like the tides. Moreover, for man's senses the term rhythm is not very appropriate unless the changes or events come in rapid succession, as in a melody or in verses. When there is a long interval it is more useful to speak of a "cycle", as in the case of sun-spots, which rise to a maximum of activity every eleven years. We mean by a rhythm a regularly punctuated discontinuity, rising from the extreme simplicity of see-saw and ding-dong to the complications of music and of growth. Sometimes what seems at first sight a very simple rhythm, like the beating of the heart, is found to be complicated when studied in detail, for the heart does not work with the monotonous regularity of a pendulum. And everyone knows that besides the alternation of high tide and low tide twice in the twenty-four hours, there are the major rhythms of spring tides and neap tides, according as the sun and moon are pulling the ocean in the same direction, at new moon and full moon, or in opposite directions, at the quarter-moons. Similarly the continual waxing and waning in the activity of bodily organs, such as liver and kidneys, is also affected by the larger rhythms of the seasons—in some animals very markedly. Often we may think of an organic rhythm as like a wavy line on which there are minor undulations both at the crest and in the trough.

If we try to group the natural rhythms, we may begin with a great series, including the cosmic periodicities, such as the revolution of a planet on its orbit and the rotation of either planet or sun on its own axis. The revolution of the spinning earth on its orbit gives us the rhythm of spring and summer, autumn and winter; the rotation of the earth on its axis gives us, as familiarly, the rhythmic alternation of day and night. As a consequence of the periodically changing positions of the earth in relation to sun and moon, there is the rhythm of the tides, which has had a far-reaching influence on animal life.

In a second group may be ranked those sequences in the life of plants and animals that are demonstrably correlated with the cosmic periodicities. This may be illustrated by the rings of growth in the stem of a tree, which are due to the difference in texture between the more porous spring wood and the closer summer or autumn wood. The alternation of two kinds of wood-forming is intelligible in the light of the different vital conditions in spring and in summer, but there are many cases where the correlation between internal rhythm and external periodicity is certain, though we cannot at present explain how it works. Thus at full moon in October or November the Pacific Palolo worm comes out of its retreats on the shores of Fiji and Samoa and spawns profusely on the surface of the sea. The Atlantic Palolo that frequents the Tortugas and other islands backs out of the crevices of the rocks and breaks off the posterior portion of its body. This rises to the surface and swims rapidly backwards, spawning as it does so. The water is so thick with slender worms that it looks like vermicelli soup; when the myriads of germ-cells are shed it appears almost milky. The headless bodies die, but the head portion, remaining in the burrow, grows a new body for the following year—a strange rhythm. The swarming occurs within three days of the moon's last quarter between June 29 and July 28. But what the precise connection between the moon and the worm may be we do not know. In some other sea-worms the egg-laying occurs regularly at the time of the spring tides in June, July, and August, and this may be associated with the abundance of food material and consequent increase of vigour at these times. Lunar periodicity in spawning is also well illustrated by one of the common sea-urchins of the Red Sea, *Centrechinus setosus*, which spawns at each full moon in the summer months. Munro Fox has shown that one and the same sea-urchin may shed its germ-cells at one full moon and have another crop ready a month later. This does not hold for Mediterranean sea-urchins, though the ancients recorded a belief to this effect.

A very striking rhythm is exhibited by a Californian smelt, called the Grunion. These little fishes come out of the water on the second, third, and fourth nights after the highest tides in spring, usually

in April. The females, with males in attendance, wriggle tail foremost into the sand and lay about two thousand eggs several inches below the surface, enclosed in a kind of capsule. The fertilised eggs develop in the sand, but the fry are not liberated until the capsule is washed out by the high tides associated with the next full moon. This is a very adaptive rhythm that works out profitably for the race of Grunions.

A third group of rhythms may be defined to include cases where there is more or less independence of the external punctuation, as is illustrated by the migratory impulse in many animals. Very interesting is the rhythmic behaviour of the tiny green worm, Convoluta, of the beach at Roscoff, in Brittany, that comes to the surface of the sand when the tide goes down, and retreats again at the first splash of the incoming flow. It will continue this rhythm for a week at least in a tideless aquarium. There has been some internal registration that lasts for a short time even when there is no ebb and flow to emphasise the external gravitational periodicity.

Everyone is familiar with the rise and fall of leaves in the morning and in the evening respectively. The regular movements are well seen in plants like clovers, French beans, and acacias, but they are of general occurrence; and it is interesting to find that their regularity sometimes lasts although the external stimulus of day and night is no longer operative. That is to say, the regular change from the day position to the night position takes place for a time even when the plants are kept in constant darkness or in constant illumination. The tune goes on, so to speak, though the conductor has ceased to beat time.

Semon reared acacias in an alternation of 12 hours' light and 12 hours' darkness, and then shifted them to periods of 6 hours' (or of 24 hours') light and darkness. He found that they exhibited an interesting compromise, as if the established rhythm was struggling with a much altered stimulation. The seedlings of acacias that had become accustomed to the 12–12 alternation were exposed to artificial days and nights of six hours, but they exhibited the 12–hour rhythm slightly modified. Yet it was a rhythm that they had not experienced as separate individuals! Some others that were exposed to continuous darkness or to continuous illumination exhibited the 12-hour rhythm for a time. But it soon became indistinct, and abnormal conditions set in. It would be interesting to have a critical repetition of these experiments.

A fourth group of rhythms may be defined to include those internal regularities which have more or less lost, if they ever had, any obvious connection with external changes. In illustration may be mentioned the beating of the heart, the loading and unloading of gland-cells, the see-saw of growing and not growing, of working and resting, of waste and repair. This kind of rhythm is characteristic

of life. If energy is used up in work, there must follow a period of recuperation. Perhaps there are deeper reasons still, involved in the colloidal structure of the living matter; and here it should be noticed that in some simple and apparently straightforward chemical reactions, such as that between an acid and a metal, there is distinct evidence of a rhythmic, not a continuous progress. Perhaps we may go deeper still to the fact that energy is emitted or absorbed by an atom not continuously, but as little bundles, parcels or "quanta"!

MIGRATING AS A PARTICULAR ILLUSTRATION

Migration is a seasonal mass-movement between a breeding and nesting place and a feeding and resting place. It is best illustrated among birds; but it also occurs among fishes, such as the salmon; among reptiles, such as the marine turtles; and among mammals, such as reindeer. It is to be distinguished from occasional mass movements whose spur is over-population, as in the well-known case of the Scandinavian lemming; and from the great movements which some fishes, like herring, illustrate, when they follow their food from one area in the sea to another, the shifting of the food-organisms being due to changes in currents, temperature, and the like. To apply the word migration to such movements is to blunt a good term. Nor should it be applied to cases where animals find a congenial area unoccupied and proceed to colonise it, as rats have done in Britain. Migration is like a tide between winter quarters, where there is recuperation and rest, and summer quarters, where there is breeding and brooding; and for birds the rule is that they nest in the colder part of their migrational range. Thus swallows and storks which winter in Africa may nest in North Europe; while penguins which spend the summer on southern seas usually brood on the shores of the Antarctic Continent. Typical migration implies a double journey—to and from the breeding-place, but we may legitimately speak of the migration of eels, although the adults die after spawning and the return journey is confined to their offspring.

Since bird-migration is emphatically a seasonal phenomenon it is interesting to contrast a tropical country, where the seasons are but slightly marked, with a north temperate country, where there is sharp punctuation. Mr. Beebe notes that a square mile of forest in British Guiana may shelter as many different kinds of birds as there are on the British list, that is to say, rather over four hundred. But whereas far over three hundred of the British birds are *emphatically* migratory, this cannot be said of more than forty or so in the Guiana square mile. In other words, our summer visitors are birds whose constitutions exclude the possibility of breeding in a tropical country and of wintering in a northern one.

Let us now focus the familiar fact that the birds of a north temperate country may be classified, as regards their migration, into five groups. First there are the summer visitors, such as swallow and swift, cuckoo and nightingale, who arrive from the south in spring, nest within our bounds, and return in late summer or in autumn to their southern and south-eastern winter quarters. Second, there are the winter visitors, such as fieldfare and redwing, snow-bunting and great northern diver, who nest in the Far North but come south in winter. A few of these winter visitors may occasionally nest in this country, as the snow-bunting well illustrates. Third, there are the birds of passage in the stricter sense, like some of the sandpipers, the great snipe, and the little stint, which usually rest for a short time only in a country like Britain, on their way farther south or farther north, as the case may be. Fourth, there are the "partial migrants", a group larger than used to be supposed. Partial migrants are those birds which are never unrepresented in the country in question, yet some go while others stay. Thus in many parts of Scotland there is not a month in the year when lapwings are not to be seen, yet the "ringing method" has proved that there is a regular autumnal migration from the sterner Scotland to the more genial Ireland. Similarly, there are always goldfinches in the south of England, yet there is a regular migration southwards in October and a corresponding return in April. Fifth, there are the strictly resident birds, such as, in Britain, the red-grouse and the house-sparrow, to take a sacred and a profane example. It is not meant that even the red-grouse remains stationary, year in and year out; but, apart from artificial introductions, it is not known outside of Britain. On the other hand, although the hedge-sparrow may be called resident in Britain, it is migratory on the Continent. Many of our so-called resident birds turn out to be partial migrants, as is true of rooks, skylarks, and song-thrushes. It is well to avoid thinking of these convenient groups in any hard and fast way, for a species that is resident in one part of the country may be a migrant in another; and the summer visitors of a northern country are the winter visitors of a southern one; or vice versa. To the five groups referred to, namely, summer visitors, winter visitors, birds of passage, partial migrants, and residents, there may be added a group for "casual vagrants" such as the North American killdeer-plover, which has been recorded a few times in Britain, or better-known stragglers, such as Pallas's sand-grouse and the waxwing.

Since there are hundreds of different kinds of birds in the Northern Hemisphere, and a great variety of climatic and other conditions, it is well to avoid rigidity in our pictures of bird-migration. Thus, while there is a clear contrast between the spring movement northwards *from* warm countries and the more impressive autumn movement southwards *to* warm countries, it must be

admitted that migratory movements are spread over the greater part of the year. And again, although the tide flows on the whole north in spring, and ebbs to the south in autumn, there are many diagonal movements; and the autumnal flight of many European birds is from east to west, to begin with at least. Moreover, though there are favourite migration-routes, such as along coast-lines, chains of islands, and river-valleys, it must be recognised that the advance and retreat are often general over broad belts of country. One other caution at this stage may be permitted, that while we are sure, from marked birds, that the migration flight may cover several thousand miles, as in the case of the European swallows and storks that have been found wintering in South Africa, the range may extend for only a short distance. Yet the phenomena are the same whether inconspicuous or grandiose. One of the grandest is that of the Pacific golden-plover, which returns across the pathless sea from the breeding-places in Alaska to the winter quarters in Hawaii.

The facts of bird-migration are interesting, and it is a pity that they have been at times exaggerated. This has certainly been the case in regard to the velocity of flight, the estimates of which have sometimes reached 250 miles an hour! It may be safely said that migration velocities of over 50 miles an hour are rare; and there is no warrant for supposing that migrating birds sustain that accelerated flight which they show for a short time when in pursuit of prey. Migrating crows seem to fly at a rate of about 30 to 45, falcons at 40 to 48, geese at 42 to 55, ducks at 44 to 59 miles per hour. As to the length of uninterrupted flight, there is no possibility of resting (except on the sea) on or near the direct route from Alaska to Hawaii, some 2,000 miles; but so long a flight without a break is probably an altogether exceptional, though not unique, feat. Even strong birds like storks take many rests on the lands over which they travel in their autumnal flight from North Europe to South Africa. It is probable that 200 miles is good work for a migrating stork, and that its day does not exceed eight hours. The record for actual length of migrational range is to the credit of the Arctic tern, which may spend our winter in the summer of the Antarctic Circle!

According to the famous Heligoland observer, Gätke, migrating birds usually travel at great altitudes, perhaps 20,000 feet, though he admitted that there is also much migration at low levels, as in the case of hooded crows, starlings, and skylarks. But Gätke's estimates were based on theoretical and fallacious assumptions, and the actual observations made by airmen show that few birds are encountered at levels above 3,000 feet. Lucanus concludes that most flight takes place below 1,300 feet, and that flight above 3,300 feet is exceptional. Meinertzhagen concludes that the few birds met with above 5,000 feet are the exception, and that the

bulk of migratory flight goes on below 3,000 feet, whether by day or by night. It will be understood that the altitudes referred to are estimated as above *ground*-level. There is no doubt that swallows cross the cols of the Alps at a height of 10,000 feet and more, or that others cross the passes of the Himalayas at heights of 18,000 feet at least, above *sea*-level.

In recalling the main facts of bird-migration, we must conclude by referring to the contrast often marked between the northerly spring flight to the nesting-places and the southerly autumnal flight to the winter quarters. The vernal flight is often more impetuous and continuous, and sometimes its route is more direct than that followed in autumn. In many species the males arrive earlier than the females, and may select a nesting "territory" before their future mates arrive, as is well known in the case of warblers. The last to arrive in the summer quarters may be immature birds that will not pair that season. The autumn movements are often on a grander scale, for the ranks have been increased by the young birds of the year. There are often preliminary congregations and false starts; the young birds may go off first; but the adult cuckoos hurry away a month or more ahead of the young ones, whom they have never known.

PROBLEMS OF BIRD-MIGRATION.—There is no doubt that the facts of bird-migration are becoming clearer every year, but they raise many deep questions that we cannot as yet satisfactorily answer. The whole subject bristles with brain-stretching problems.

Our first question is in regard to the nature or true inwardness of this yearly journeying of so many birds between summer and winter quarters, between nesting-places and resting-places. If we visited a northern country and found that most of the inhabitants went in winter to the South of France, but spent the summer in the Scottish Highlands, we might say: "How very intelligent, to arrange to have two summers in the year". May we say the same for the birds that "change their season in the night and wail their way from cloud to cloud down the long wind"? But it is impossible to take this generous view, for though birds are sometimes able to put two and two together, and profit by experience, we must remember that for many generations our summer visitors have known no winter in their year. They cannot by intelligence provide against the entirely unknown. Whatever may be the answer to our question, it is not in the word intelligence. Yet we must be careful not to think that birds are *unintelligent* in their migration or in any other activity.

But it may be suggested that the success of the migratory flight depends on a tradition kept up from generation to generation. We must admit that the migrants do not meditate about their flight,

but perhaps they imitate their seniors. Yet this won't do either; for what are we to make of the fact that many young birds leave us in autumn in advance of their parents?

On the whole it seems that we must call bird-migration *an instinctive custom*. Instinctive means inborn, not requiring to be learned, engrained deeply in the hereditary make-up. Hive-bees build a honeycomb instinctively; birds migrate instinctively. It is not merely that the urge to migrate is rooted in the constitution, there is an inborn capacity for obeying the impulse in an effective way—some unusual sense of direction. One of the arguments in support of this view is that inexperienced young birds often set out alone on their long journey to an unknown goal. Another argument is that the migratory custom is seen in many kinds of creatures at very different levels of brains and mentality—in mammals, like reindeer and seals; in reptiles, like sea-turtles and sea-snakes; in fishes, like salmon and flounder; in the land-crabs also, which return every year from their inland haunts to spawn in the sea. A large part of the answer to our first question is in the mysterious word *instinctive*.

In the course of thousands of years migrating has come to be part and parcel of the constitution of many birds; therefore it must have had great advantages. There must have been good reasons why birds with a strong migratory instinct succeeded best, while those with a weak migratory instinct were sifted out. Part of the answer to this second question must be that in north temperate countries it is a great advantage to avoid the cold, the storms, the scarcity, and the short daylight of winter. And while the southern winter quarters are well-suited for rest and recuperation, they are places to get away from when summer comes, with its drought and glare. Especially for nesting there is an attractiveness in the cool northern haunts, where there is abundance of water, shade, daylight, and midges.

Our third question is somewhat like the second, and yet it is different: What are the immediately present causes that liberate the instinct to migrate? The advantage of a cool nesting-place in the distant north cannot pull the trigger which sends the swallows from South Africa to Britain in early summer. What are the immediate causes?

After a British eel has been feeding and growing for five or six years in the pond, it becomes restless, and begins to make its way down the river, whence it reaches the sea, and proceeds on its long journey, perhaps as far as the Bermudas. Now we know that there are changes in the eel's body and blood that pull the trigger of its migratory impulse; and the same is true for birds. There are internal trigger-pullers or stimuli in both cases, though we do not as yet know very much about them.

But there are also outside influences, which work hand in hand with the internal impulses. The changes of the seasons are in some measure the instigators of migration. Our summer visitors begin to feel in autumn the increasing cold, scarcity, storms, and darkness. In spring they may be provoked to return to the north by the increasing heat and glare in their winter quarters. Yet we must not think of these outside changes as *compelling* the birds to migrate; they simply help to release an instinctive impulse or internal prompting that has become enregistered in the race. This is a difficult idea, and one of the reasons is that as man has very few of these instinctive impulses, he does not find it easy to understand creatures in which they are very powerful.

In some cases migration is a social activity, for the migrants may gather in great flocks and fly away together. So we must not exclude the possibility that migrants of the same kith and kin excite one another, and that some may be much more susceptible than others to the internal and external trigger-pulling. Some young black-headed gulls which we hatched out and reared at college and afterwards set free in a comfortable garden, where they were well supplied with food, became interested at the time of migration in their kindred who flew overhead, and they eventually joined them. Matthew Arnold has a beautiful picture of a captive stork who sees his fellows flying south:

> And as a stork which idle boys have trapped,
> And tied him in a yard, in autumn sees
> Flocks of his kind pass flying o'er his head
> To warmer lands and coasts that keep the sun,
> He strains to join their flight and from his shed
> Follows them with a long complaining cry.

HOW MIGRATION BEGAN.—Our fourth question is: How did migration begin? In all probability the evolution of bird-migration is wrapped up with the history of climate. There were genial ages long ago when our summer visitors were resident birds throughout the north temperate countries of Europe. But slow changes of climate towards cold made it difficult for certain types to face the severer winter. So they flitted for short distances southwards in autumn, returning in spring to nest in cooler places with abundance of water and food. As the change of climate became more and more pronounced, the distance of the autumnal journey would have to be increased; and it is reasonable to suppose that callous or foolhardy or stupid birds, who would not take a hint, were sifted out of the race. A premium would be put on sensitive birds, on strong fliers, on keen vision, on powers of picturing scenery and reviving the picture. Thus the migratory custom might gradually evolve.

In thinking of the origins of migration, we must also remember

the broad fact that an almost universal problem in the North is how to meet the winter. Some creatures lay up stores and others put on fat; some sink into coma and others hibernate; some increase the thickness of their coat and others put on whiteness. But the neatest of all the solutions of the winter problem is migration—circumventing the winter entirely.

Not to be forgotten is the tendency that many animals have to scatter or disperse from territories that become overcrowded after the numbers have been increased by breeding. And another hint is to be found in the natural history rule that a new generation is cradled in the ancestral haunt of the race. The land-crab goes far up the hills, but it comes back to the sea to spawn. Open sea turtles, which had terrestrial ancestors, come back to the sandy shores to lay their eggs. So in other cases and so with the migrant birds, the cradle is in the ancestral home.

The fifth problem is that of way-finding. No doubt there is much mortality in migration. Some migrants lose their way on the pathless sea and perish of hunger; some are driven by storms far from their normal course; some are fatally attracted to lighthouses and dash themselves against the windows. And yet the larger fact is that the migration is usually successful; the travellers reach their winter quarters, and ringing experiments prove that they sometimes return year after year to the place of their birth. How do they find their way?

It must be allowed that birds sometimes utilise landmarks—mountain-ranges, river-valleys, chains of islands. Visual acuteness often counts for something. Fogs are well known to be much against success. Carrier-pigeons, so clever at their geography, get their early lessons by day. Yet keen sight cannot be more than part of the answer, since many birds migrate in the dark and cross great tracts of ocean where there are no landmarks. It has been shown that terns transported in closed baskets on board ship into unknown waters may sometimes return within a few days to their nests, even from a distance of 800–1,000 miles. But we must confess that we do not know how it is done.

Some naturalists still adhere to the theory that the success attending migration must be due to the cumulative inheritance of the results of experience. But it is not certain that this kind of hereditary entailment is ever possible; and it is difficult to say what sort of experience could be gained by birds that migrate in the darkness at great heights and over the trackless sea.

Nor can we lay much stress on the tradition theory, that those birds will lead well in 1930, who followed well in 1929 and 1928. For the young birds often leave before their elders.

Thus we seem almost compelled at present to suppose that birds are in high degree hereditarily endowed with a sense of direction,

which may, of course, be supplemented by visual or by some other sensory acuteness. In any case, bird-migration still bristles with brain-stretching problems.

NOTE ON THE STIMULUS TO MIGRATION.—If we grant that the migration of birds is an old-established custom, correlated with or enregistered along with constitutional rhythms in the internal economy of the body, and if we set aside the problem of its origin, an estimate of the advantages that it confers, and the puzzle of way-finding, there remains a question that many of us have asked: What are the seasonally recurring factors that pull the trigger? There are reasons for discounting food shortage, as also the changes in temperature and pressure, for a state of readiness to migrate is often manifest before the three factors alluded to have become well-marked. In a recent study by Mr. William Rowan, emphasis is laid on the changes in the length of the day. The stimulus may be due to the shortening daylight in autumn and the lengthening daylight in spring. To the objection that northern birds wintering in the Southern Hemisphere are subject, before their northward flight, to shortening instead of to lengthening daylight, and that those wintering on the Equator are not subject to any stimulus of this kind, it may be answered that the "photoperiodism" may operate not at particular moments, but rather in securing the regularity of the bird's physiological cycle.

But Mr. Rowan has not only argued, he has experimented. He captured some juncos (finches) in Alberta in the course of their southward migration, and kept them in two outdoor aviaries, one of which was equipped with two 50-watt electric bulbs (of ordinary glass), while the other was left to natural illumination. In both cases the birds were well fed, and were found to thrive in spite of the severity of a winter normally unexperienced. But the effect of artificially lengthening the illumination in the one aviary, while it was naturally decreasing in the other, was to bring about a premature re-activation of the reproductive organs. The result of this, when the birds were liberated, was interesting, though the data are still too imperfect to allow of quite secure conclusions. The birds kept in the natural aviary, with their gonads at the normal winter minimum, did not migrate. They remained in the vicinity and were usually recaught. Their thwarted migratory instinct had passed into abeyance, a frequent phenomenon in animal behaviour But when the birds from the illumined aviary, with their gonads in a state more appropriate to spring, were liberated at the same time as the others, namely, in mid-winter, they disappeared. The migratory activity had apparently been re-activated at an inappropriate season because the artificial light conditions had effected an acceleration of the normal physiological cycle.

MIGRATION—IN OTHER ANIMALS.—While it is among birds that migration is seen in its most typical form, it is also a custom with many other animals. But there has been an unfortunate tendency to apply the term in a loose way to many movements of animals that are very different from the migrations of birds. Migration in the strict sense, defined in reference to its most typical expression in birds, is a racial custom, enregistered in the animal's constitution, and takes the form of a periodic or seasonal mass-movement between a breeding-place and some other environment in which breeding does not occur. In other words, migration implies that the animals concerned have two haunts in which they regularly live at different seasons of the year, or at different phases of their life. It is illustrated among seals, turtles, toads, by such fishes as salmon, and by such crustaceans as land-crabs. It is a pity that such a clear and convenient term should be blurred by an application to phenomena which it does not fit. The following should be excluded from the rubric of migration. (*a*) Roaming movements in search of food, whether at short intervals or at different seasons, are not migratory. (*b*) Mass-movements, of fishes, for instance, that are not related to reproduction, but are instigated by marked changes in the physical conditions, or in the dependent distribution of the food, should not be mixed up with migrations. (*c*) Even impressive trekking, coerced by increase of numbers and by exhaustion or destruction of the food-supply, is not migratory. The march of the Scandinavian lemmings, when they have exhausted the vegetation of a district, is no more a migration than is a devastating swarming of locusts. (*d*) Also to be excluded are the movements of larval animals from their birthplace to another more suitable environment, as when the larvæ of shore animals become pelagic and return to littoral waters as their metamorphosis is or is not being completed. It would be just as unprofitable to apply the term migration to the movement of the May-flies out of the water, or the movement of the liver-fluke's cercariæ out of their water-snail host. The word has been similarly misapplied to the striking march of Procession Caterpillars from the pine-trees along the ground—a march that continues until they find suitable soft soil into which to burrow for pupation. (*e*) Also to be separated off are the various forms of extension of geographical range, which may be very impressive as in the case of the incursions or "invasions" of Sand-Grouse into Britain, or may be, as is more frequent, very gradual and hardly perceptible from generation to generation. The passive diffusion of gossamer-spiders by the wind, or of marine animals by oceanic currents, is certainly not migration. Yet the term is persistently applied to the often striking mass-movements of butterflies and some other insects, which are usually, if not invariably, dispersal-movements. Even Elton calls attention to the way in

which the slow dispersal of animals may be brought about by "migration", meaning the spreading of the environment, as in the extension of the tundra zone or the forest belt. But this application of the term is unnecessary, and it can be avoided by speaking of the extension or shrinkage of a particular type of environment, or by using some other phrase, like "ecological succession".

The distinctive features of true migration are the following. (*a*) It is a racial custom, enregistered in the constitution, but activated by particular stimuli, both internal and external. (*b*) It is of regular recurrence, either seasonal and periodic, or involved in the animal's attainment of a particular age or state. (*c*) It is a geographical or topographical change from one haunt to another, one being the breeding-place. And in typical cases there is a return journey, as is familiar in the ebb and flow of the feathered tides of migrant birds. In some cases, such as the Common Eel, the adults die after spawning, and the return journey is thus confined to the larval stages.

Here we would quote a few clear sentences from A. L. Thomson's *Problems of Bird-Migration* (1926). "To deserve the description 'migratory', in its strict sense, movements need not necessarily have a very great geographical amplitude, but at the least they must involve a definite change of locality. They must be purposive in that the change of scene is associated with some definite advantage which serves as its *raison d'être,* and there must be return movements to the original area. They must be periodic in that they correspond to some recurrent change either in the environmental conditions themselves or in the animal's reaction thereto. True migrations are changes of habitat, periodically recurring and alternating in direction, which tend to secure optimum conditions at all times."

MAMMALS.—Perhaps the best instances of true migration in mammals are to be found among seals, though the Common Seal (*Phoca vitulina*) in Britain is practically a resident species. More typical is the Alaska Fur Seal (*Callorhinus alascanus*), which winters as far south as California, and returns in spring across the North Pacific for 2,000 miles to its remote breeding-place on the fog-hidden Pribilof Islands. Cetaceans, being more thoroughly adapted to marine life than the Pinniped Carnivores, do not need to come to the shore to breed, yet there is some evidence of their migratory movements. The same may be said in regard to reindeer, but the facts are not very easy to understand. The Newfoundland Caribou (*Rangifer terranovæ*) moves in autumn from the stormy uplands, where the "reindeer moss" and the like are apt to be buried deep in snow, to the less strenuous conditions towards the south coast of the island. The southward movement takes place after the mating season, usually late in October, and is somewhat leisurely,

at a smart walking pace, unless the wintry conditions set in very abruptly. The reindeer travel for the most part by day, along more or less well-trodden paths, in relatively small companies, and in single file. Of interest is the fact that the earlier companies consist mainly of does, fawns, and young stags, while the later companies consist mainly of the big stags. In the spring there is a return movement, when the does are heavy with young, which is somewhat divergent from the avian migration scheme. Too much must not be made of this difference, yet it must be admitted that the so-called reindeer "migration" approximates to the mass-movements of gregarious Ungulates of steppe-like areas when the dry season compels them to "follow the grass". Moreover, some Caribous are practically resident both in the northern and the southern parts of Newfoundland. On a somewhat similar betwixt-and-between level are the seasonal movements of Rhesus and Hanuman monkeys in India. They move in the hot season from the plains to the hills of Nepal, and return to the low grounds in the cold season, bringing their young with them. There is no doubt that some of the bats take gregarious flights on a large scale, while others may pass in crowds every evening from the mainland to an adjacent island, just as starlings are known to do. But it is very doubtful whether any of the mass-movements of bats can be included within the rubric of migration. Willey refers to an interesting "Box and Cox" alternation in Ceylon, where certain fruit-eating bats rest among the palms of an adjacent islet during the day, but go to the main island to feed at night, while flocks of crows alternate with them by roosting on the islet palms by night and visiting Ceylon by day. But nothing is gained by calling this migration!

REPTILES.—Some of the marine turtles are good instances of true migrants. Thus the Loggerhead (*Caretta caretta*), a carnivorous species of tropical and intertropical seas, visits many sandy shores to deposit the eggs on the beach. The newly hatched young ones make persistently for the sea, moved, as G. H. Parker has experimentally shown, by a constitutional obligation to go down a slope and to walk in the direction of the most open low horizon, be this the right way to the sea or no. The vegetarian Green Turtle (*Chelone midas*), which deposits its eggs on sandy beaches in the West Indies, has a short migrational range, not known to exceed 50 miles. It spends ten months of the year in the relatively shallow coastal waters, for though it is sometimes found in the open ocean, its normal haunt is bound to be not very far from the seaweed-growing region. Some of the sea-snakes are true migrants, for they come periodically to the shore to give birth to their young ones among the rocks.

AMPHIBIANS.—A familiar sight in spring in some places is the march of toads from a considerable distance to a particular pond or marsh, where they pair and spawn. When, some months later,

the tadpoles have become small toads, there is a journey in the opposite direction, the parents having returned inland some time previously. The same is true of the Crested Newt in Britain, but the distances covered are not so great as in the case of the toad. Similarly in the common Grass Frog there is a summer movement of the young ones from the water to the fields, whither the parents have preceded them some time before. The return to the water, or to the vicinity of the water, is autumnal, not vernal as in toads, and it is not so well-defined.

Fishes.—The term migration has been mistakenly applied to many mass-movements of fishes, e.g. herring and mackerel, which have no connection with a return to a particular spawning-ground or type of spawning-ground. These non-migrational movements are largely explicable in terms of changes in the distribution of the planktonic and other organisms on which the fishes feed, or, what may come to the same thing, in terms of changes in temperature, salinity, oxygenation, carbon dioxide tension, and so forth. No doubt such changes may sometimes serve as external stimuli to true migrational movements, but no mass-movement of fishes should be ranked as migrational, unless it is directly concerned with approaching or leaving a spawning area, as with the salmon.

True migration is familiarly illustrated in the salmon (*Salmo salar*). The eggs are liberated, often in midwinter, on suitable gravelly stretches of the river-bed. There are successive stages of alevins, fry, parr, and smolts. The last, when over two years old, pass down the rivers to the sea, usually in the early summer months. A vigorous nutritive life is spent in the sea, where the food consists largely of young herrings and mackerel; and the salmon may remain there for several years. Adolescent salmon, which have not quite put on the adult characters, are called grilse, and are normally three and a half years old, having descended to the sea as smolts the previous year. These may ascend the rivers as grilse and may even spawn as grilse; but the grilse stage is often passed through in the sea, so that the maiden fish which are entering the fresh water for the first time are often, in the strict sense, salmon. The adult salmon eat very little, if at all, in fresh water; they return to the sea, if they can, after spawning. In some cases it has been proved by marking that salmon return from the sea to their own particular native river.

When a migratory fish comes inshore or ascends the rivers to spawn, the term anadromous is used, with its counterpart catadromous when the spawning occurs in deepish salt water; and other useful terms for different types of movement have been defined by Meek. In contrast to the salmon, the case of the flounder (*Pleuronectus flesus*) may be mentioned. In many places it has become a freshwater fish, and may be found flourishing in stretches of river

many miles from the sea. But the flounder must return to its native salt water to spawn, and the sea is also the scene of the larval life and of the metamorphosis. Fully formed young flounders ascend the rivers.

The researches of Schmidt show that the chief breeding area of the European Eel (*Anguilla vulgaris*) is in deepish water in the south-western part of the North Atlantic, somewhat to the north of the West Indies. Thence the transparent larvæ (Leptocephali) gradually make their way, helped by currents, towards the European coasts, including those of the Mediterranean and the Baltic. As they approach these coasts, being over two years and a half old, and having traversed, it may be, two thousand miles, they undergo a remarkable metamorphosis, from a knife-blade-like to a slender

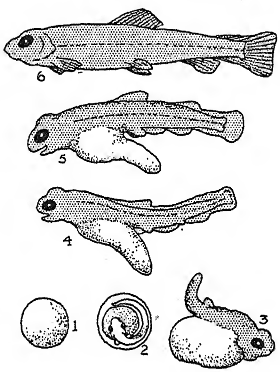


FIG. 18.

Life-history of Salmon. From specimens. 1, The egg; 2, the developing embryo within the egg; 3, the newly hatched alevin, with yolk-sac protruding; 4, 5, subsequent alevin stages; 6, the young fry, having absorbed the yolk-sac. All approximately natural size.

cylindrical shape, and are known as elvers. These ascend the rivers and often pass to lakes, feeding voraciously and growing quickly, continuing their nutritive life for five to eight years, the females taking longer to assume the characters of maturity. The physiological restlessness that then sets in prompts a migration down the rivers and out to sea, the long journey taking several months. The contrast to the avian scheme of migration is noteworthy, since the adult eels seem to die after spawning, so that there is no return journey to the fresh waters save for the next generation. Similarly the large marine lamprey (*Petromyzon marinus*), ascends the rivers to spawn and succumbs soon afterwards. The larvæ, known popularly as "niners", technically as "Ammocoetes", remain larvæ for three years or so, and then, attaining to adult characters, they go down to the sea to put on flesh. The basal fact in the interpretation

must be that lampreys were originally freshwater animals, as most of the species always remain, whereas the Common Eel had originally a deep-water marine home, and took secondarily to an exploration and exploitation of the freshwaters. It is interesting to note that in the interior of New York State *Petromyzon marinus* does not go down to the sea, but passes from river to lake, and from lake to river. Such secondary telescopings of the typical life-history are very significant.

INVERTEBRATES.—Most of the so-called migrations of Invertebrates are misunderstandings. The mass-movements of butterflies and dragonflies and other insects are very impressive, but the whole trend of the evidence is in favour of regarding them as occasional dispersal movements. On the other hand, there is genuine migration in the movements of land-crabs (Geocarcinus) and robber-crabs (Birgus) from the interior to the shore. In the sea the larvæ are hatched out, and in the sea all the youthful stages are passed. From the sea there is a return of the adults to their inland retreats, and later on they are followed by their hereditarily adventurous offspring. This is migration.

ANIMALS IN THEIR HAUNTS

It is part of the pleasant task of ecology to consider living creatures in relation to their environments, and we wish here to think of the major haunts of life—the Open Sea, the Shore of the Sea, the Deep Sea, the Freshwaters, the Dry Land, and the Air—with its birds and insects.

PELAGIC.—The pelagic fauna includes all the animals of the open sea, both drifters (Plankton) and swimmers (Nekton). The physical conditions in which they live are very favourable—there is room for all, sunshine without risk of drought, and an evener life throughout the day and throughout the year than is to be found elsewhere except in the abysses of the deep sea. Moreover, the minute pelagic Algæ afford an inexhaustible food-supply to the animals. It is not surprising, therefore, to find that the open sea has been peopled from the earliest times of which the rocks give us any life record.

The fauna is representative, exhibiting great variety of types, from the minute Noctiluca, which sets the waves aflame in the short summer darkness, to the giants of modern times—the whales. It includes a few genera of Foraminifera, rich in species, most Radiolarians, Dino-flagellata, many Infusorians, Medusæ and Medusoids, Siphonophora and Ctenophora, many "worms," a few Holothurians, a legion of Crustaceans, a few Insects (Halobatidæ), such Molluscs as Pteropods, Heteropods, and many of the Cephalopods, such Tunicates as Salpa and Pyrosoma, many fishes, a few turtles and snakes,

besides some well-known birds and mammals. There are also hosts of *larval* forms which are pelagic for a time.

The fauna of the open sea is representative, but there are few of the types which we can suppose to have lived there always. It may be that forms like the minute water-fleas have been there almost from the first, but most bear the impress of lessons which the open sea could never have taught them.

Pelagic animals tend to be delicate and translucent; many are phosphorescent. The number of species, differing from one another within a relatively narrow range, is often enormous; thus about 5,000 species of Radiolarians are known. The huge number of individuals, which frequently occur in great swarms, is equally characteristic. Perhaps both facts indicate that the conditions of life are relatively easy, as is also implied in the limitless food-supply afforded

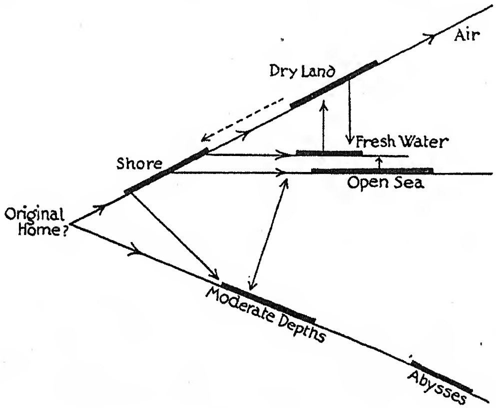


FIG. 19.

Schema of the Great Haunts of Life and their Possible Relations with one Another.

by the unicellular Algæ. The pelagic fauna is richest in the colder seas.

ABYSSAL.—Through the researches of the *Challenger* and similar expeditions, we know that there is practically no depth-limit to the distribution of animal life, though the population is denser at moderate depths than in the deepest abysses, and though there is probably a thinly peopled zone between the light-limit and the greatest depths. We know, too, that there are abyssal representatives of most types from Protozoa to Fishes, and that the distribution tends to be cosmopolitan, in correspondence with the uniformity of the physical conditions.

The abyssal fauna includes some Foraminifera and Radiolarians, many flinty sponges, some corals, sea-anemones, and Alcyonarians, a few medusæ, annelids and other "worms" on the so-called red clay,

representatives of the five extant orders of Echinoderms, abundant Crustaceans, representatives of most of the Mollusc types, and peculiarly modified Fishes, some with small eyes, others with large eyes, which probably catch the fitful gleams of phosphorescence.

As to the physical conditions, the deep-sea world is in darkness, for a photographic plate is not influenced below 250–500 fathoms; it is extremely cold, about the freezing-point of fresh water, for the sun's heat is virtually lost at about 150 fathoms; the pressure is enormous—thus at 2,500 fathoms it is about $2\frac{1}{2}$ tons per square inch; the cold water in sinking from the polar regions brings down much oxygen; it is quite calm, for even the greatest storms are relatively shallow in their influence; there are no plants (except perhaps the resting phases of some Algæ), for typical vegetable life depends upon light, and not even bacteria, otherwise almost omnipresent, are known to flourish in the great depths. A strange, silent,

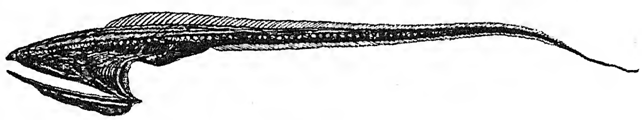


FIG. 20.

A Deep-sea Fish, Gastrostomus, with an enormous gape, the lower jaw being hinged very far back, an adaptation to the reduced opportunities for food-capture in abyssal conditions. After Murray and Hjort.

cold, dark, plantless world! The animals feed upon one another and upon the débris which sinks from above.

We do not clearly know when the colonising of the depths began, but there is much to be said for the view that an abyssal fauna was, at most, scanty before Cretaceous ages. But whensoever the peopling of the abysses occurred, it must have been gradual. It is likely that most of the pioneers migrated outwards and downwards from the shore region (in a wide sense), following the drift of food; it is possible that others, e.g. some Crustaceans, sank from the surface of the open sea. The boreal character of many deep-sea animals has been often remarked, and it is plausible to suppose that there was a particularly abundant colonisation in the Polar regions, and a gradual spreading towards the Equator as the Poles became colder. Perhaps the richness of the fauna at the Equator may be thought of as in part due to the meeting of two great waves of life from the Poles.

The abyssal conditions of life tend to uniformity over vast areas, just as in the open sea. But, on the whole, life must always have been harder in the depths than on the surface. The absence of plants, for instance, involves a keener struggle for existence among animals. Thus, although many abyssal forms, e.g. sea-anemones, live a passive sedentary life, waiting for food to drop into their mouths,

the majority are less easygoing. The deep sea has been a sterner school of life than the surface.

LITTORAL.—At a very early date the shores were peopled, and the fauna is very rich and representative. From the strictly Littoral zone, exposed at low tide, with its acorn-shells and periwinkles, limpets and cockles, to the Laminarian zone (to 15 fathoms), with its sea-slugs and oysters, where the great seaweeds wave listlessly amid an extremely keen battle, to the Coralline zone (15–40 fathoms),

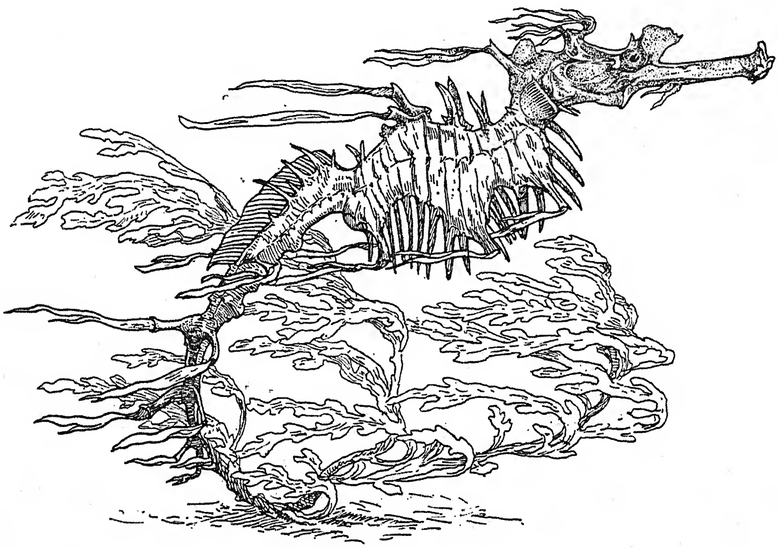


FIG. 21.

One of the Sea-horses (*Phyllopteryx eques*), whose tassels give it a remarkable resemblance to the seaweed among which it lives. After Gunther.

with its carnivorous buckies, what variety and abundance, what crowding and struggle!

There are Infusorians and Foraminifera, horny, flinty, and calcareous Sponges, zoophytes and sea-anemones, many "worms", starfishes and sea-urchins, crabs and shrimps, acorn-shells on the rocks and sandhoppers among the jetsam, a few insects about high-tide mark, sea-spiders clambering on the seaweeds, abundant bivalves and gasteropods, sea-squirts in their degeneracy, besides fishes, a few reptiles, numerous shore birds, and an occasional mammal. The shore fauna is thus very representative, rivalling in its range that of the open sea, far exceeding that of the abysses.

The conditions of life on the shore are in some ways the most stimulating in the world. It is the meeting-place of air, water, and land. Vicissitudes are not exceptional, but normal. Ebb and flow of tides, fresh-water floods and desiccation under a hot sun, the

alternation of day and night, felt much more markedly than on the open sea, the endless variations between gently lapping waves and blasting breakers, the slow changes of subsidence or elevation—these are some of the vicissitudes to which shore animals are exposed. The shore is rich in illustrations of keen struggle for existence and of life-saving shifts or adaptations, such as masking, protective coloration, surrender of parts, and "death feigning". We may think of it as a great school where many of the primary lessons of life, such as moving head foremost, were learnt.

The Very Varied Freshwater Fauna.—Compared with the total surface of the earth (197,000,000 square miles) the fresh waters occupy but a small area (1,800,000 square miles), i.e. a little over one per cent., yet they exhibit great variety. One has only to think of lakes and tarns, ponds and pools, wells, ditches, streamlets,

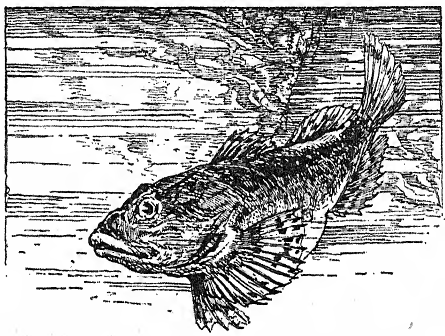


Fig. 22.

A Typical Littoral Fish (*Cottus scorpio*), or Bullhead. From a specimen.

and rivers, to call up pictures from this world-wide heterogeneity; and in the lake at least, geologically distinguished from the pond not by size but by depth, it is often necessary to distinguish littoral, open-water, and abyssal zones. Thus parts of Lake Baikal have a depth of 760 fathoms, compared with which the vast Caspian is almost a pond.

In the eighteenth century there was an enthusiastic and illuminating study of freshwater animals, led by men like Leeuwenhoek, Roesel von Rosenhof, Réaumur, and Trembley, whose industry and insight are well appreciated in the late Prof. Miall's *Early Naturalists*. With the beginning of the nineteenth century, however, the attractiveness of marine zoology began to make itself felt, and soon claimed the attention of the majority. Yet after a long period of relative neglect the freshwater fauna is once more the subject of lively interest, the revival having been in no small degree due to the thoroughness of Miall's studies on the life-histories of freshwater

insects. Many lakes have been provisionally surveyed, and a number of freshwater biological stations have been founded.

Physical Conditions.—There is considerable diversity in the chemical substances dissolved in the water, and this sometimes exerts a limiting influence on the distribution of organisms. Thus freshwater crayfishes do not survive in water that has a very low proportion of lime salts; though freshwater mussels, with much heavier calcareous shells, seem to be strangely indifferent to this.

Of great importance is the fact that in the cold and temperate zones the surface temperature in lake and pond is highest for about 280 days in the year, and lowest for the remainder. As fresh water has its maximum density at 4° C. and expands below that till it freezes, there is in winter a rise of the expanding bottom water to the surface, where it adds to the thickening of the sheet of ice. This sheet retards further cooling, and in most cases prevents the total freezing of the lake or pond. Thus, for about 85 days of the year, the bottom has the highest temperature, and this helps greatly towards the survival of the freshwater fauna in north temperate countries. The intricate rhythmical fluctuations in the temperature of lakes and large rivers have been much studied, especially in the United States; and correlated with waxing and waning in the density of the aquatic population.

There is rarely much penetration of light below six fathoms, but the sensitive photographic plates show that the chemical rays are still appreciable at depths of fifty to ninety. Blue water, which is purest, is the most penetrable; green water, with its innumerable microscopic and ultra-microscopic particles, is less penetrable; and least conducive to life is yellow-brown water, which is darkened by much humic acid, from peaty soil and the like. The degree of illumination is of obvious biological importance, since it determines the depth-range and rate of multiplication for minute green Algæ, like Diatoms and Desmids, on which minute Crustacea and the like in turn depend.

Zones of a Lake.—The littoral lacustrine zone includes all the well-illumined shallow water near shore. Among its familiar plants are duckweed (Lemna), pondweed (Potamogeton), water-buttercup (Ranunculus), water-lilies (Nymphæa), mare's-tail (Hippuris), bog-bean, and bulrushes. The land-building by the growth and soil-formation of such vegetation is often so marked as to make notable extensions into an old lake area, apart from the delta-like deposits from its tributary streams. There is often an abundance of filamentous and single-celled Algæ; and of much importance as a food for animals is the minute detritus broken from the shore vegetation.

The littoral fauna includes birds like waterhens and grebes, in some countries turtles and terrapins, amphibians like newts and frogs, in their young stages especially, small fishes like sticklebacks

and minnows, water-snails and freshwater mussels, an occasional water-spider and many water-mites, small crustaceans, leeches, wheel animalcules, Turbellarian worms, Hydra, Spongilla, Infusorians and Amœbæ—a very representative series of animals. Some of them, such as shallow-water molluscs, have free-swimming larvæ in the open lake.

The open water includes a multitude of minute Algæ which form the chief food-supply of the small drifting or Plankton animals, notably the Entomostracan Crustaceans, popularly called water-fleas. Far from shore there may also be great growths of the rootless Utricularia, partly insectivorous, and sheets of the Water Lobelia. Also able to effect photosynthesis are a number of greenish Protozoa, e.g. Peridinium and Ceratium, which have chlorophyll, or sometimes partner Algæ. Of great interest is the waxing and waning of the lake-plankton, varying sometimes with temperature and weather, sometimes with changes more obscure—even with the moon. To be distinguished from the drifting Plankton is the more energetic, relatively more katabolic Nekton, such as very active water-mites at one extreme and large lake-trout at the other. In Lake Baikal there are actually seals, pointing to an ancient connection with the sea.

Thirdly, the dark deep waters of the lake contain characteristic animals, such as the Rhizopod Arcella, a reddish species of Hydra, a considerable variety of Planarian, Nematode, and Oligochæte worms, a blind Cyclops, a deep-water bivalve (Pisidium) and snail (Limnæus), some light-shy mites, and a few fishes like the sluggish Burbot (*Lota vulgaris*) and the giant barbel (Silurus).

INTER-RELATIONS.—The economy of a lake or a pond depends on the balance between the photosynthetic "producers" and the animal "consumers", with bacteria as links that convert the remains or waste-products of animals into nitrogenous substances and carbon dioxide which may be utilised by green plants. The fact that some animals devour others and may be themselves devoured in turn, does not affect the general proposition that the animal population depends in the long run on the plants. As in the sea, the "nutritive chains" may be long or short: thus merganser—trout—water-snail—water-weed would be an average chain of four links, while swan—water-weed would be a common short one.

Many of the inter-relations are of great interest. Thus the freshwater mussels require for the continuance of their race the unconscious co-operation of some freshwater fish, such as the minnow, on the skin or gills of which the ("glochidia") larvæ of the mollusc fix themselves and pass through a metamorphosis, eventually dropping off into the mud, perhaps far from the place where they effected fixation. On the other hand, there can be no continuance of the Bitterling (*Rhodeus amarus*) unless the female fish, which has a very

long ovipositor, inserts her eggs into the outer gill-plate of the mussel, where they undergo a prolonged development, eventually giving rise to larvæ which make their way out of their temporary host.

Several kinds of small fishes devour the aquatic larvæ of mosquitoes, and thus check the spread of malaria. The Californian *Gambusia* is thus being introduced along the French Mediterranean lagoon region. The freshwater snail *Lymnæus truncatulus* is the British host of the larval stages of the liver-fluke which causes "rot" in sheep. The burbot is one of the hosts of the larval stage of the Broad Tapeworm (*Bothriocephalus latus*), one of the most troublesome parasites of man.

Utilisations of such increasing knowledge of the life-histories of

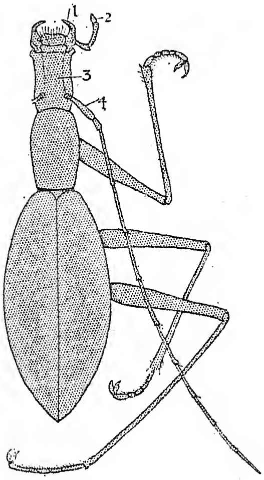


FIG. 23.
Cave Insect, with reduced eyes, but enlarged antennæ (4), and mouth-parts (1 and 2).

inimical species are thus now in active progress. (See section on *Biology in Medicine.*)

MINOR FAUNAS.—(*a*) *Of brackish water.*—We are warranted in speaking of a brackish-water fauna, because of its uniformity in widely separated regions. It does not seem to be a mere physiological assemblage, varying in each locality, but rather a transition fauna of ancient date, a relic of a littoral fauna once more uniform. The fact is that the power to live in brackish water is not very common; it runs in families.

(*b*) *Cave fauna.*—In America, thanks very largely to the labours of Packard, about 100 cave animals are known; in Europe the number is about 300, the increase being largely due to the occurrence of about 100 species of two genera of beetles in European

caves. In the famous Mammoth Cave of Kentucky, which has over 100 miles of passages, with streams, pools, and dry ground, there are over 40 different species of animals. The temperature is very equable, varying little more than a degree throughout the year; it is, of course, dark; and there are no plants other than a few fungi. Thus the conditions present some analogy with those of the deep sea. The fauna is of much interest to evolutionists, for we wonder how far the peculiarities of the cave-animals, e.g. absence of coloration and frequent blindness, are due to the cumulative effect of the environment and of disuse, or how far they represent the survival of germinal variations, and the result of the cessation of natural selection along certain lines. Have the seeing animals

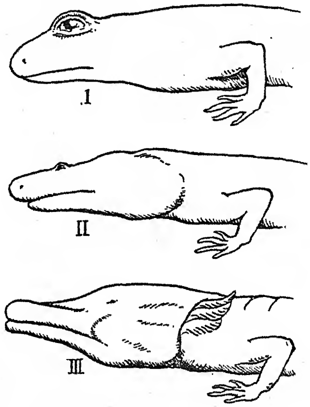


FIG. 24.

Three Closely Related Newts, living in different conditions of life: I, in full illumination; III, in darkness, where the eye is practically absent; and II, in intermediate conditions, where the eye is small.

found their way out, leaving only the blind sports, which crop up even in daylight? Or is the loss of eyes the result of disuse and absence of stimulus? Or again, if it be granted that pigment is an organic constitutional necessity, e.g. a waste-product, while coloration is explicable as an adaptation wrought out in the course of natural elimination, then the question arises, whether the cessation of natural selection—a condition awkwardly called "panmixia"—which might account for the disappearance of the *coloration* when there is no premium set upon it, can also account for the loss of *pigment*—that is, of a character which was not acquired in the course of natural selection. (See Beddard's *Animal Coloration.*) Our only answer at present is that there is need for experiment.

(*c*) *Parasitic fauna.*—It seems legitimate to rank together those animals whose habitat is in or on other organisms, from which they derive subsistence, without in most cases killing them quickly, if at

all, or, on the other hand, rendering them any service. Among ecto-parasites there are such forms as fish-lice and many other Crustaceans, numerous insects such as lice and fleas, and Arachnids such as mites. Among endoparasites there are Sporozoa, some Mesozoa, many Nematodes, most Trematodes, all the Cestodes, many Crustaceans, insect larvæ, and Arachnids.

The parasitic habit implies degeneration (varying according to the degree of dependence), great nutritive security, prolific reproduction, and enormous hazards in the fulfilment of the life-history.

Parasitic animals must be distinguished: (*a*) from epiphytic or epizoic animals which live attached to plants or animals, but are in no way dependent upon them, e.g. acorn-shells on Norway

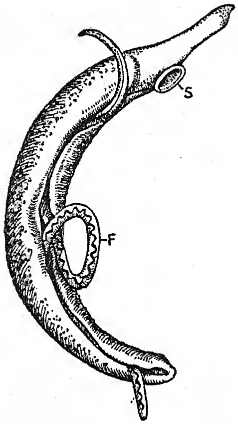


FIG. 25.

Dimorphism in Bilharzia Worm (Schistosomum). The male, about $\frac{3}{5}$ inch in length, carries, in a ventral groove, the longer, narrower female (F); S, posterior sucker. After Looss.

lobster; (*b*) from commensals, who live in some degree of external partnership, but without in any way preying upon one another, e.g. crab and sea-anemone; and (*c*) from symbions, who live in close internal partnership, or symbiosis e.g. Radiolarians and Algæ. But between these habits there are many gradations, and from close association there is always an easy transition to parasitism.

TERRESTRIAL.—The colonising of dry land has doubtless been a gradual process, as different types wandered inland from the shore, or became able to survive the drying up of freshwater basins. The fauna includes some Protozoa, e.g. *Amœba terricola,* which lives in moist earth, some of the Planarians, Nematodes, Leeches, Chætopods, and other "worms", a few Crustaceans like the wood-lice (Oniscus), many insects and Arachnids, a legion of slugs and snails,

most adult Amphibians, most Reptiles, many Birds, and most Mammals. Among Vertebrates certain fishes are of interest in having learned to gulp mouthfuls of air at the surface of the water, to clamber on the roots of the mangrove trees, or to lie dormant through seasons of drought. But among Vertebrates, Amphibians were the first successfully to make the transition from water to dry land.

It is important to bear in mind that many a stock may, in the course of its evolution, have passed through a variety of environments. Thus the thoroughly aquatic Cetaceans were probably derived from a land stock common to them and to the Ungulates, and may have passed through a freshwater stage. Without going further back, we have here an illustration of the zigzag course of evolution.

We cannot believe in any abrupt transition from the shore to terra firma. It has been a slow ascent, slow as the origin of dry land itself. Thus mud-inhabiting worms, dwellers in damp humus, bank-frequenting animals, those which find a safe retreat in rottenness or inside bolder forms, dot the path from the shore inland. Many have lingered by the way, many have diverged into culs-de-sac, many have been content to keep within hearing of the sea's lullaby, which soothed them in their cradles.

Simroth, in his work on the origin of land animals, seeks to show that hard skins, cross-striped muscle, brains worthy of the name, red blood, and so on, were acquired as the transition to terrestrial life was effected. Let us take the last point by way of illustration. Iron in some form seems essential to the making of hæmoglobin, but iron compounds are relatively scarce and not readily available in the sea; they are more abundant in fresh water, and yet more so as the land is reached. Therefore it is suggested that it was when littoral animals forsook the shore for the land, via freshwater paths, that iron, in some form, entered into their composition, became part and parcel of them, helped to form hæmoglobin or some analogous pigment, and thus opened the way to a higher and more vigorous life.

Returning to the Sea.—Pliny divided animals into Aquatilia, Terrestria, and Volatilia, the creatures of water, earth, and air. But among the "Aquatilia" it is necessary to distinguish the primarily and secondarily aquatic. Thus no one supposes that jellyfishes and starfishes and cuttlefishes, to take only three examples, ever lived anywhere but in water; whereas whales, turtles, and sea-snakes are types whose ancestors lived on land. The primarily aquatic animals breathe the oxygen that is dissolved in the water, and they are cold-blooded, their body-temperature tending to be the same as that of the surrounding medium. Another feature in the primarily marine backboneless animals, and in the gristly fishes like sharks and skates, is the osmotic equilibrium between the fluids of

the body and the sea-water outside. Thus the same kind of animals may have salter blood in the Mediterranean than in the North Sea.

The sea is the original home of living creatures—the cradle of all the races; and it was from the sea that the primary freshwater animals had their origin. Some of them, like the pond-mussel and the river-crayfish, betray this in the osmotic tension of their body-fluids, which is much higher than that of the surrounding water. There are various interesting ways in which freshwater animals preserve this marine inheritance from over-dilution, e.g. by increasing the activity of their kidneys, or by decreasing the permeability of the surface-membranes by which the surrounding water tends to seep into the body.

Our problem is not with the indigenous animals of the sea, nor with the early colonists of the fresh waters, nor with the interesting land animals, like the water-spider, that have found a secondary refuge in ponds and streams; we think of the return to the sea after ages of sojourning on land. Among backboned animals there are several distinct groups of mammals that have followed this policy—the Cetaceans (whales, dolphins, porpoises), the Sea-cows or Sirenians (dugong and manatee), the seals and sea-lions, and the now rare sea-otter (Enhydris). Even the Common Otter may swim from the mainland to an island, and the polar bear may swim in open water for many miles. Among birds that have become secondarily marine we may rank the Antarctic penguins; and in the North the likewise flightless Great Auk, now extinct. All the members of the auk family, like guillemot and razorbill, may be called pelagic birds, and the petrels are even finer conquerors of the open sea. The Storm Petrels—"Mother Carey's Chickens"—are the smallest of web-footed birds, but they are at home in mid-ocean, and never come to land except at nesting-time; and almost the same may be said of the largest web-footed bird, the Albatross, which has a spread of wing up to eleven feet eight inches.

Among reptiles there are the sea-snakes, venomous fish-eaters of the open ocean, which do not come ashore except to bring forth their young among the rocks. The edible turtles that feed on sea-weeds keep near shore; but the fish-eaters frequent the open waters, except at the breeding season, when perforce they must come to sandy beaches to bury their eggs. It will be understood that whereas a whale can bring forth its young one in the sea, the oviparous birds, and such aquatic reptiles as are oviparous, must go back to the old home to find a cradle for their eggs. The unhatched embryo of a turtle, like that of a bird, breathes dry air, which diffuses through the egg-shell and into the blood-vessels spread out on the embryonic membrane called the allantois. In the sea-snakes there is viviparity; and the young ones must be able from the first to use their lungs on the surface of the water.

One of the two giant lizards of the Galapagos Islands, Amblyrhynchus, is unique in venturing into the sea. Unlike its inland cousin, Conolophus, which has learned to eat the fruit of the prickly-pears, the seashore lizard creeps out on the half-covered rocks, where it holds firm with its twenty claws and browses on the seaweed. Geologically marooned on very inhospitable islands, these giant lizards have obeyed the spur of hunger, and have found two very diverse solutions of their bread-and-butter problem—the one eating prickly-pears and the other the sea-ware. The case of Amblyrhynchus is peculiarly instructive; for it shows how necessity might impel a thoroughly terrestrial animal to return to the sea.

There are no marine amphibians; and some think it is stretching a point to claim the salmon as a freshwater fish which has returned

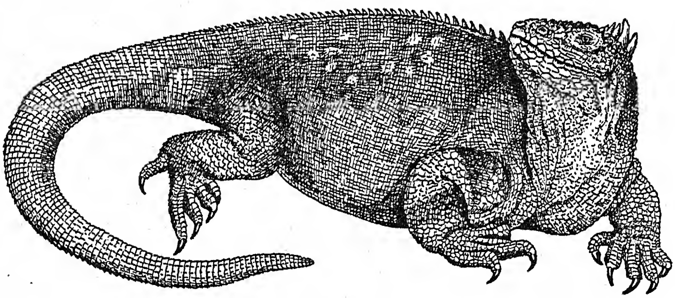


FIG. 26.

The Giant Lizard (Amblyrhynchus), of the Galapagos Islands. After Beebe. It is about four feet long and brilliantly coloured, and also remarkable in its habit of browsing on seaweed on the surf-splashed rocks.

to the sea for nutritive purposes, a procedure the very reverse of that illustrated by the common eel. So, with a bow to the marine mites and the extraordinary open-sea bugs (Halobates), known as sea-skimmers, we may close the list of animals that have returned to the sea.

Whenever an animal makes a marked change of habitat, such as passing from land to sea, we cannot but expect special adaptations, and some examples may be of interest. Thus, as to locomotion, though we may not clearly understand how the changes were effected, we see the fitness of the whale's torpedo-shaped body with its perfect stream-lines, its frictionless skin, and the fashioning of the tail into a powerful propeller that does not need to go round. Changes so drastic as these leave many tell-tale evidences, such as the buried vestige of a hip girdle and the dwindled relics of a hind leg; and they may have required long ages for such regression. It is probable that seals and sea-lions are newcomers to the water as compared with Cetaceans, for the moulding of their bodies and

limbs has not gone nearly so far. Moreover, in the seal-tribe the mothers have to go ashore to bring forth and suckle their offspring.

Compared with the remodelling of the whale's body, the transformation of the penguin or the turtle is relatively slight. The penguin's wings have become stiff oars, but the strong keel on the breastbone is enough to show how far this old-fashioned-looking and flightless bird is from the antique running birds, such as ostriches, where there is no keel at all. The typical clawed limb of the terrestrial Chelonian has become the nail-less flipper of the sea-turtle, and the sea-snakes show an interesting side-to-side flattening of the tail, sometimes carried on to the posterior body as well, the better to grip the water in the lateral thrusts of swimming.

The blubber of a Cetacean is an exaggeration of the subcutaneous deposit of fat that is common in mammals. It makes the creature more buoyant; it conserves the precious animal heat which is apt to be lost in the cold water; it is also a store of calories for evil days. The thick skin and the dense fur, often double in the seals and their relatives, has also a heat-conserving value.

Since the lung-breathers that return to the sea must inspire dry air at the surface, we can understand the fitness of the whale's power of taking enormously big breaths, of storing oxygenated blood in wonderful networks (*retia mirabilia*) of blood-vessels, and of rapidly increasing its stock of red blood corpuscles. And, speaking of respiration, we see great interest in the fact that some marine turtles and sea-snakes have superficial capillary networks in the cavity of their mouth and about their jaws—a quaint return towards gill-breathing, though of course quite distinct.

The impression of the plasticity of life grows on us as we study the animals that have returned from the land to the sea. See how the sharp points of the seal's teeth are tilted backwards, the better to grip the fish; how the nostrils in Cetaceans can be closed in diving; how the mother-whale can give its baby a big drink of milk at a time; how the kidney often has a very large lobulated excretory surface; how the retrogression of the olfactory area of the brain is associated with the development of something better, and so on. The fact is, that all these animals that have returned to the sea are but specially interesting instances of the universal truth that an organism is a bundle of adaptations—unified.

AËRIAL.—The last region to be conquered was the air. Insects were the first to possess it, but it was long before they were followed. The flying-fishes vibrated their fins above the foam as they leapt; the web-footed tree-frogs (Rhacophorus) and various lizards, with the skin spread out on elongated ribs, began to swoop from branch to

branch; some of the ancient Saurians flapped their leathery skin-wings; a few arboreal mammals essayed what the bats perfected; and the feverish birds flew aloft gladly.

Perhaps a keen struggle among insects, or such events as floods, storms, and lava-flows would prompt to flight; perhaps it was the eager males who led the way; perhaps the additional respiratory efficiency, produced by the outgrowth of wings, gave these a new use. Perhaps the high temperature of birds—an index to the intensity of their metabolism—may have had to do with the development of those most elaborate epidermic growths which we call feathers. But we must still be resigned to a more or less ingenious "perhaps".

EVOLUTION OF FAUNAS.—The problem of the evolution of faunas is still beyond solution, but various possibilities may be stated.

(*a*) According to Moseley, "the fauna of the coast has not only given origin to the terrestrial and freshwater faunas, it has throughout all time, since life originated, given additions to the Pelagic fauna in return for having received from it its starting-point. It has also received some of these Pelagic forms back again to assume a fresh littoral existence. The terrestrial fauna has returned some forms to the shores, such as certain shore birds, seals, and the polar bear; and some of these, such as the whales and a small oceanic insect, Halobates, have returned thence to Pelagic life.

"The deep sea fauna has probably been formed almost entirely from the littoral, not in the most remote antiquity, but only after food, derived from the debris of the littoral and terrestrial faunas and floras, became abundant in deep water.

"It was in the littoral region that all the primary branches of the zoological family-tree were formed; all terrestrial and deep-sea forms have passed through a littoral phase, and amongst the representatives of the littoral fauna the recapitulative history, in the form of series of larval conditions, is most completely retained."

(*b*) According to Agassiz, Simroth, and others, if one may venture to compress their views into a sentence, a littoral fauna was the original one, whence have been derived, on the one hand, the Pelagic and abyssal faunas; on the other hand, the freshwater and terrestrial faunas.

(*c*) According to Brooks, a Pelagic fauna was primitive, whence have been derived the tenants of the shore and the inhabitants of the deep sea. To the latter, however, a possibility of ascending again is not denied.

(*d*) Sir John Murray has emphasised the importance of "the mudline"—the lower boundary of the littoral area—as an important headquarters of animal life, and as the area from which the abysses were peopled. The possibilities have been expressed in Fig. 19.

FROM POLE TO POLE

Let us make a short selection in simple illustration of the way in which living creatures must be considered in their geographical environment.

The Northern Forests.—With our eyes shut we should be able to see from Pole to Pole—the Arctic Ocean with its icebergs and bird-islands, the Barren Grounds or Tundra, the great Coniferous Forests, the Steppes, the arable midlands and meadows, the hot deserts, the Tropical Forests, the southern Steppes or Pampas, and the Antarctic continent. According to the meridian that we select, the sequence will differ in detail, but there is a general resemblance in the succession from Pole to Pole. Even over the waters of the ocean there is a zoning, so that we are surprised to find, as Bruce of the *Scotia* did, Arctic terns within the Antarctic Circle, or an albatross in England.

The zone we wish first to get glimpses of is the Northern Forest, a vast belt, as everyone knows, to the north of Europe, Asia, and America, sometimes 800 miles in width. It lies between the Barren Grounds to the north and the Steppe Lands (or meadow-lands) to the south. In Siberia, where it stretches for over 3,000 miles, from the Ural Mountains to the Pacific Ocean, it is called the Taiga.

As contrasted with the warm rain-forests, of which Mr. Beebe has given us such vivid pictures, where vegetation reaches its climax, both in luxuriance and variety, the northern forests consist of only a few different kinds of trees—largely conifers. This means that the severity of life-conditions has greatly restricted the number of possible tenants. There is a check to the ascent of sap, for the soil is cold through half the year, the water is sour with humic acid, and there is not much evaporation from the thick-skinned leaves into the cool air. Thus growth is slow. Difficulties are increased by the fierce winds of winter, and the heavy snows have eliminated those trees with spreading foliage that do not allow what falls to slide off easily. In a southern region, where snowstorms are rare, it is interesting to observe after a heavy fall that cedar-like trees stand uninjured, while many of their broad-leaved neighbours are borne to the ground or badly maimed. So in the northern forests there is a predominance of pine and spruce, larch and cedar. Shooting up in the thick shelter between these conifers there are slender, long-drawn-out birches, rowans, alders, and hazels, which could not survive by themselves. In her *Forest, Steppe, and Tundra,* Miss Haviland compares these stripling trees to the lianas and climbers of the tropical jungle. "They grow as straight and close-set as the

bars of a cage; and although often no thicker than the little finger, they make human progress difficult and slow."

The picture of the northern forest is in very sombre colours. So crowded are the trees that it may be dark on a summer day; the undergrowth is often limited to berry-bearing plants like blaeberries, or to bog-moss and lichen; sometimes there is nothing but a deep carpet of needle-like leaves. The branches are hoary with lichens, and the trees die of senescence while young in years. There is an all-pervading odour of mouldiness. Except when the summer-visiting birds are in possession, there is a depressing silence. Sometimes everything seems asleep except the mosquitoes. A belt of monotony stretches round the world.

Relieving the gloom in summer are the birds which batten on the mosquitoes, while others linger long enough to get some of the berries. Miss Haviland has a beautiful touch in picturing the forest birds at dawn, perched on the tops of the trees, waiting for the light. An ousel, far to eastward, begins to pipe faintly, and the good news spreads through the woods, until every tree is a fountain of song. "It seems as if the great wooded shoulder of the earth, rolling eastwards into the sunrise, awakes one songster after another, until Asia and Europe, from Pacific to Atlantic, are linked together by a chain of thrushes' music."

Among the characteristic forest birds may be mentioned the crossbill, whose beak becomes twisted in early life so as to form a very effective instrument for splitting fir-cones; the attractive waxwing with the quaint red tips to some of its feathers; the woodpeckers who hammer for tunnelling grubs on the decaying stems, the handsome mealy redpolls and scarlet grosbeaks and bluethroats, the vocal thrushes, including the fieldfare and the redwing, which come to us in winter. Then there are big game-birds like capercailzie, blackcock, and the wood-grouse that puts on horny snowshoes in the winter. In swampy places and on the river banks there are sandpipers, redshanks, woodcock, goldeneyes, and bleating snipe. While the clouds of mosquitoes and midges may make the explorer's life a purgatory, it must be remembered, as a theoretical ointment, that the flies are re-incarnated as birds. Perhaps most of the forest birds are seed-eaters, but in the swampy regions there are many illustrations of insects becoming flying fowl—say, wagtails by day and goatsuckers by night.

Another link in the nutritive chain is represented by the birds of prey, such as the diurnal falcons and buzzards, and by the owls softly flying in the darkness, which extends in the depth of the forest into what should be daylight hours. So we must correct the impression of moribund monotony by noticing the abundance of bird-life in the summer at least; and the same is true of the mammals to which the forest gives shelter. Brehm gives us vivid pictures of the

Maral Stag and the reindeer, the roe-deer and the broad-antlered elk or moose. The carnivores are represented by wolf, fox, lynx, and bear, and by smaller types, so fine of fur, like sable and ermine, mink and marten. Both tree-squirrels and ground-squirrels are much in evidence, and another typical rodent in the clearer stretches is the Variable Hare, which, like the Arctic fox and the ermine, puts on a white dress when winter comes. This may help in part as a cloak of invisibility, but its chief value is probably that it conserves the precious animal heat better than any other colour.

Very characteristic of the forest mammals is the relative frequency of hibernation, as illustrated by marmots, sousliks, chipmunks, and

FIG. 27.

Greenland Falcon (*Hierofalco candicans*), a very successful bird of prey in Arctic regions. Like many other inhabitants of the far north, it is predominantly white in colour. From a specimen.

some squirrels. These winter sleepers are imperfect in their warm-bloodedness; when the cold sets in they cannot produce enough of heat to make good what is lost; they relapse into a strange state of suspended animation, but before this grips them they obey an instinct to creep into a sheltered corner, where the temperature rises above that of the surrounding world. There they lie low, with the heart beating feebly and the breathing movements scarce perceptible. They have no income except a little oxygen, and no expenditure except a little carbonic acid gas. The process of excretion stops and the blood undergoes a marked change. The usual reactions to stimuli, or answers-back to provocations, are in abeyance. It is a strange relapse towards reptiledom, but if it is a weakness, it becomes a strength. For most of the "winter sleepers"—not that it is really sleep that they illustrate—reawaken in spring much refreshed and ready for their meals.

While three or four of the forest mammals turn white in winter

and perhaps a dozen fall into hibernation, the majority have to trek southwards before the snows and storms. We can picture the march of the deer, with the wolves and gluttons at their heels.

The Mammals of the Steppes.—Let us continue our attempt to envisage animals in relation to their characteristic haunts; the animal life of the Polar regions, the tundra, the northern forests, the mountains, the desert, the tropical jungle, and so on. The most striking book on the subject is Miss Haviland's *Forest, Steppe, and Tundra: a Study in Animal Environment* (1926); and we wish just now to think about the mammalian fauna of the Steppes.

By a "steppe" is meant a great tract of undulating grass country, "a sea of herbage", and it includes "prairies" and "pampas". One of the most characteristic, often called *the* steppe, extends eastwards, in Russia and Siberia, from the plains of Hungary to the foot of the Altai Mountains. Many of us have visited this tract of country under the enchanting guidance of Aksakoff and Tchekov; and we are always ready to go back, for there is a peculiar fascination in the steppe.

In her admirable book, Miss Haviland points out that the two outstanding physical characteristics are "the fierce extremes of the climate and the monotony of the landscape". The summer temperature may be like Morocco, the winter like Novaya Zemlya. There is heavy rainfall in spring, parching drought in summer, desiccating wind and keen frost in winter. These conditions favour grass and certain kinds of wiry herbage; they make it difficult for trees to live, except in sheltered depressions beside rivers and lakes. In May and June the steppe is a garden of mulleins, mallows, larkspurs, composites, vetches. "In July the flowers fade, the grass scorches brown, and the steppe appears like a parched stubble field." In winter the biting wind sweeps up the snow except from the hollows; and death stalks over a bare land.

The second characteristic of the steppe is the monotony. It is an open plain, with great rivers, no doubt, but scarcely broken by hills—an environment, as Miss Haviland says, that has nurtured thinkers and dreamers, just as the fierce extremes of the climate have prompted explorers, adventurers, warriors, and nomads. How does this apply to the mammals?

In a grassland one expects many herbivores—in other words, many rodents and ungulates. But the number of possible inhabitants of this type is greatly reduced by the lack of shelter, by the often torrid summer with a baking sun, and by the often frigid winter with its bitter winds. One line of survival is swift trekking; another is burrowing. Let us take the second first, with Spalax as type. It is a vole adapted to the underworld like a mole. But Spalax is

a rodent, whereas a mole belongs to the distant order of Insectivores. In Spalax the body is barrel-like; there is little in the way of tail or ear-trumpets, the strong limbs are fossorial, the eyes are small and may be degenerate, as in *Spalax typhlus*, sometimes called the blind mole-rat. In winter the Spalax burrows deeper, below the grip of the frost's fingers, and feeds on roots and bulbs, which it sometimes stores. Here, then, is a clear-cut instance of successful adaptation to difficult conditions, for Spalax conquers the steppe by becoming a creature of the underworld. The same may be said of many other burrowing rodents, such as the gregarious sousliks that make great warrens and often baulk man's efforts at steppe-conquest by devouring the crops in the fields he has ventured.

The subterranean mode of life is also illustrated by marmots, hamsters, and voles; and it is said that our hedgehog, which we do not count as a burrower, though it may shelter in rabbit-holes, sometimes digs on the other side of the Caspian to a depth of eight or nine feet—an interesting variation in habit. Perhaps to be included are several species of Pika or Piping Hares, with short vole-like ears, no external tail, and a peculiar call. We say "perhaps", because most of them resemble our Variable Hare in preferring the uplands, and some resemble marmots in living at very high altitudes.

A second solution of the steppe problem is beautifully illustrated by the biped Jerboas, such as *Alactaga jaculus*, badly called the Jumping Rabbit, and the fascinating *Dipus hirtipes*, whose tail (7 inches) is longer than its body ($4\frac{1}{2}$ inches). Their particular solution is that they have added to burrowing an extraordinary elusiveness. They take prodigious unpredictable jumps, landing neatly on their three-toed feet, the fore-limbs being held tightly against their breast. We can understand the very long and springy hind-legs, the long coalesced instep bones, the very long balancing tail, and so on; but we do not know how to interpret the fusion of five or six neck vertebræ. The atlas or first vertebra is always free, and sometimes the last; five are always fused. There is no clue in the fact that a similar coalescence occurs in whales!

Brehm describes the nocturnal jerboa with his usual enthusiasm. "After sunset, or later, if the moon be favourable, one may see the charming creature steal cautiously from his hole. He stretches himself, and then, with his little fore-limbs pressed close to his breast, hops off on his kangaroo-like hind-legs, going as if on stilts, balancing his slim, erect body by help of his long hair-fringed tail. Jerkily and not very rapidly the jerboa jumps along the ground, resting here and there for a moment, sniffing at things and touching them with his long whisker-hairs, as he seeks for suitable food." He eats what he can get—seeds, bulbs, smaller mammals, and birds' eggs. When all is quiet he hops about in a leisurely way; but on the appearance of an enemy, such as wolf, fox, eagle, or man, he puts

on such a pace that "even on horseback one could scarce overtake him. With great bounds he hurries on, jerking out his long hind-legs, with his tail stretched out as a rudder; bound after bound he goes,

FIG. 28.

Jerboas (Dipus), typical mammals of the desert and steppes. The long hind-legs are adapted for rapid bipedal progression and astonishingly long leaps—an adaptation securing safety.

and, before one has rightly seen how he began or whither he went, he has disappeared in the darkness."

The third solution of the steppe problem is illustrated by the larger mammals, such as antelopes, gazelles, the maral stag, and

the wild asses. All these trust to their swiftness and to their ability to travel quickly for long distances. They have discovered the nomad's solution—rapid trekking, away from drought, snowstorms, and dust-storms, extreme frost, and other difficulties. They are less secure, however, than the burrowers, and their numbers are declining, especially on the European Steppe. The wild horse or Tarpan, which was common when Brehm visited the Asiatic Steppes about fifty years ago, is now unfortunately extinct. Very delightful is the picture he gives of one of the wild asses, the Kiang or Kulan (*Equus hæmionus*), but it is almost confined to the lofty tablelands, to which its exceptionally thick coat is well suited.

There is a fourth contingent of mammals on the steppes—namely, the beasts of prey, who levy toll on the herbivores, both large and small. Such are the weasels and pole-cats, the wolves and foxes, the badger and the glutton. But they are rather to be regarded as raiders from the forest than as characteristic steppe mammals.

What has been said of the mammals might be said, *mutatis mutandis*, of the birds. The sand-martins may represent the burrowers; the bustards, cranes, and quails correspond to the swift jerboas; the rooks and bee-eaters follow the grazing herds; the eagles and falcons, the buzzards and harriers correspond to the beasts of prey. The ocean of grass teems with vegetarian insects, such as locusts and bugs; and these become re-incarnated in lizards and snakes, which are at home on the steppes in large numbers and in great variety.

Antarctic Animals.—In very cold weather our imaginings always carry us to polar regions, or to snowclad mountains, or to the eternal winter of the deep sea. There is some subtle reflex that makes us conjure up environments which are colder than our own; and so we often come to think of the Antarctic. As long as we keep to the open sea and the deep waters, there is an undeniable parallelism berween the fauna of the Far North and the fauna of the Far South; and this formed the basis of an almost obsolete "Bipolarity Theory", which interpreted the similarity as due to a common origin of polar marine animals in early Tertiary times from a somewhat uniform population in temperate and tropical seas. But there seems to be no need for any special theory beyond the assumption that similarly adapted types of life are likely to arise in or find their way to similar haunts.

While there are few cases of the same pelagic and abyssal species occurring in Arctic and Antarctic seas, there is a general parallelism. But this is not illustrated by the animals of the shore, and still less by those on land. In fact, the contrast between terrestrial animals in the Far North and in the Far South is very striking. Thus Bruce of the *Scotia*, in his interesting lectures, used always to emphasise four facts: that there were no land mammals in the Antarctic regions, that there was only one kind of land bird (the sheath-bill), that there

were no freshwater fishes, and that there was no vegetation in the interior of Antarctica except a few lichens and mosses. What a contrast to the Arctic regions with their foxes and hares, reindeer and lemmings, bears and wolves; and the same contrast holds in regard to land-birds and insects and vegetation.

In thinking of this striking contrast between the two polar regions we must keep in mind the broad fact that the Antarctic has a more "oceanic climate", that is to say, the seasons are less sharply defined. In the south the winters are less cold, but the summers are less warm. It is the abundance of sunshine in the short northern summer that saves the Arctic from the lifelessness of Antarctica. In one faunistic feature, however, the Arctic and the Antarctic regions agree, and that is the abundance of life in the sea. Thus the population of small crustaceans and other open-sea organisms is far denser than in tropical waters. This somewhat surprising fact finds more than one explanation. The prevalent cold slows the pace of life, putting a brake on metabolism, so that there are more generations living at the same time; in cold waters there are fewer oceanic Bacteria than in the Tropics, and that may mean a more economical utilisation of the nitrogenous compounds in the water, especially by the "floating meadows" of green Algæ; and thirdly, the cold polar waters are more abundantly oxygenated than those at a higher temperature, and oxygenation favours life.

Let us now single out a few of the characteristic Antarctic animals. On a frozen continent, the size of Europe and Australia, there is not a single mammal, for there is nothing to eat; but in the seas there are, or recently were, abundant whales and seals. The whales are represented by finners, humpbacks, threshers, blackfish, and the Southern Right whale, a true Balæna. A fine list, but unless more effective international protection is soon secured, the years are numbered for all these southern cetaceans; and then the whaling companies will wind up ingloriously.

The Antarctic seals include some very fine types, the Weddell seal, the Ross seal, the crab-eating white seal, and the sea-leopard. Bruce speaks of the swiftness and litheness of the last species, which makes a habit of catching penguins in the sea. Very remarkable, but only occasionally penetrating the pack-ice, is the sea-elephant, one of the most extraordinary of mammals. The male may be 20 feet long, and he can dilate his nose into an upstanding proboscis that rises to a height of about a foot! The females and young males bellow like bulls, and the full-grown males have a roar like the "noise made by a man when gargling"! At the breeding season, when their nose stands up with rage, the males fight furiously with heavy-weights of their own size; but we are told that the elephant seal is at heart inoffensive and of mild disposition. There is something just a little comical about these giants, for when they drag themselves with

difficulty out of the water on to the Kerguelen shore, "the vast body trembles like a great bag of jelly, owing to the mass of blubber by which the whole animal is invested, and which is as thick as it is in a whale". When the tremulous colossuses settle down for a siesta they throw scraped-up sand over their body, for they are very susceptible to sunburning!

Had it not been for unpardonable shortsightedness, ruthlessness, and greed, there might have been to-day a much greater representation of the valuable sea-lions or fur-seals of the south, the Antarctic representatives of the Northern Fur Seal (*Otaria ursina*), of whose unsurpassable soft under-fur few of us are worthy. Man cannot be called either an intelligent or a conscientious trustee of his kingdom!

In Arctic lands there is an abundance of flowers and insects, but these are conspicuous by their absence in the Antarctic. The scarcity of insects worth catching accounts for there being no land-birds, except the sheath-bills. Also to be remembered is the rarity of suitable nesting-places on the Antarctic continent, and Bruce speaks of "the obvious difficulty of fragile land-birds getting to Antarctic lands across the wide expanse of the stormy Great Southern Ocean".

The white sheath-bills or kelp pigeons, which are practically the only Antarctic land-birds, form a small family, perhaps linking the plovers to the gulls. They fly strongly and sail beautifully over the sea; on land they walk about and court like pigeons. They feed on mussels and anything of that sort that they can pick up on the shore, and they make rough-and-ready nests in nooks among the rocks. Their name refers to a peculiar sheath on the upper bill.

But when we pass from land-birds to sea-birds the Antarctic picture changes. Not only are there several different species of penguins and petrels, but the number of individuals is immense. It testifies to the abundance of crustaceans in the cold waters. On the South Orkneys alone there are said to be millions of penguins, and over 25,000 nesting pairs of the Snowy Petrel, which sailors call the Cape Pigeon. Besides penguins and petrels, both of fascinating interest to ornithologists, the Antarctic list of marine birds includes two skuas, two terns, a gull and a shag. As an instance of the insurgence of life, can anything surpass the occurrence of Arctic terns as summer visitors within the Antarctic Circle—one of the *Scotia's* notable discoveries?

These sketches of Northern Forests, steppe-lands, and the Antarctic must suffice as illustrations of one of the most interesting and instructive lines of ecological study.

INTER-RELATIONS OF ORGANISMS

It is a familiar fact of observation that living creatures have become in various ways inter-linked, so that the circle of one life intersects

the circles of many other lives. Gilbert White's letter on the influence of earthworms in Nature, written in 1777, was the precursor of Darwin's *Formation of Vegetable Mould*, published more than a hundred years afterwards (1881); and central to both is the idea of the correlation of organisms—the vital linkages that bind living creatures together in mutual dependence and interaction. This is the idea of the Web of Life.

The frequency of these inter-relations is partly due (*a*) to the necessary linkages between the Animal Kingdom and the Plant Kingdom, for all animals are in the long run dependent on plants; and (*b*) to the fact that the scheme of Animate Nature implies a sequence of re-incarnations or re-embodiments, one organism depending on another for sustenance. Here also account must be taken of the rôle of Bacteria in the circulation of matter.

But some other factor is needed to account for the *frequency*

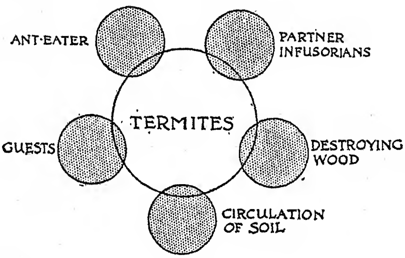


FIG. 29.

Diagram of Inter-relations, suggesting how the circle of one life, e.g. Termites, intersects many other circles, e.g. guest-insects, ant-eater enemy, partner infusorians, the trees destroyed, and the soil.

of vital linkages in Animate Nature, and that factor is to be found in the spurs implied in the struggle for existence, and from this we can hardly separate *the dynamic quality* of the vigorous organism. The struggle for existence is due to the rapid multiplication shown by most living creatures, to the changefulness of the physical environment, and to the scheme of nutritional changes that evolution has wrought out; and it cannot be separated from the quality of insurgence and unsatisfiedness that marks most organisms that do not simply follow the line of least resistance. The spur of struggle and the urge for "more" are so incessant that living creatures are rarely slow to use opportunities, whether consciously realised or but reflexly reacted to. Thus has arisen the great variety of inter-relations, in which some advantage is gained on one side or on both sides by means of some sort of vital linkage.

INTER-RELATIONS CLASSIFIED.—An attempt must be made to classify the numerous inter-relations which are so charac-

teristic of the World of Life. The first four that we shall mention are on a somewhat different plane from the others, being more fundamental, almost like biological axioms.

(1) There is the fundamental balance between animals and green plants. For green plants by their photosynthesis make food for themselves and for the animals that are directly or indirectly dependent on them for sustenance. Moreover, to the photosynthetic process we owe most of the oxygen of the air, on which almost all life depends.

(2) Then there are the nutritional chains that bind different organisms into a sequence of re-embodiments. Thus Diatoms and Peridinid Infusorians form the food of the Copepod Crustaceans of the open sea; these form the staple food of mackerel; which may be eaten by man. As we have mentioned elsewhere, a pound of cod's flesh requires for its making ten pounds of large whelk or "buckie", each pound of which corresponds to ten pounds of sea-worms, each pound of which corresponds to ten pounds of animalculæ and organic particles. So that a pound of cod's steak represents a thousand pounds of "sea-dust".

(3) From these two fundamental facts it follows that there will be many minor instances of balance, to some of which we have referred in the section on the Balance of Nature. Thus in a given region there will be an established balance between the carnivores and the herbivores, between the insectivorous birds and the insects, and so forth.

(4) Of great importance are the linkages effected by help of Bacteria, which complete many a circle both on land and sea. The dead body of the animal or of the plant is decomposed by certain putrefying Bacteria, and there is a liberation of water, carbon dioxide, and ammonia, all of which may be re-absorbed by plants and used over again. In many cases, the ammonia, formed by the putrefaction of the proteinaceous substances of the dead organism, is changed by specific Bacteria into nitrites, which are changed by others into nitrates, and these, absorbed by the roots, form the ordinary source of nitrogen for green plants. These plants are eaten by animals, and so the world goes round. Liebig was one of the first to have a clear view of this *circulation of matter*.

(5) In various ways in the course of evolution one living creature has become dependent on another for the continuance of its race. Thus many flowering-plants cannot produce fertile seeds unless the appropriate insect-visitor dusts the stigma with the pollen carried from the stamens of another blossom of the same species. Similarly with the scattering of seeds by birds and by some mammals; the necessary sojourning of the larva of the freshwater mussel in some fish like the minnow, and of the young of the Bitterling (a Continental freshwater fish) in the gill-plate of the mussel; and the indispensa-

bility of certain ants to the successful development of the Large Blue butterfly.

(6) Allied to the preceding is the linkage established when two animals, widely apart on the scale of being, share a common parasite. Thus the freshwater snail (Limnæus) and the sheep are hosts of the juvenile and adult stages, respectively, of the liver-fluke; other freshwater snails (Planorbis, Bulinus, etc.) are hosts of the larvæ of Bilharzia, which may become a formidable parasite in man; the mosquito carries the malaria-organism, and the Tsetse-fly carries the cause of Sleeping Sickness.

(7) A number of linkages may be grouped together as Shelter and Positional associations, where an organism is advantageously sheltered, or lifted, or carried by another. A quaint fish, Fierasfer, shelters inside a Holothurian (sea-cucumber), and another Amphiprion, within a sea-anemone. Many orchids and other plants live as perched epiphytes on trees; many small sponges, zoophytes and worms are carried about on the shells of crabs and other locomotor marine animals; the sucking-fish or Remora profits by being transported by a shark or a turtle to which it may temporarily attach itself; climbing plants use their neighbours as convenient supports. It is not necessary to over-exert one's ingenuity in finding a utilitarian justification for each and every instance of epiphytic or epizoic association, for many of them are probably casual and unimportant, witness a bunch of ship-barnacles attached to the flattened tail of a sea-snake. There is probably little significance on either side in the presence of unicellular green Algæ on the shaggy hairs of the tree-sloth. The attached organisms referred to are simply expressing their constitutional tendency to fix themselves to other organisms or to things, and the attachment is not always appropriate. Yet it must be borne in mind that at some new crisis in the struggle for existence, what was indifferent may become vital, and even of survival value.

(8) Commensalism is conveniently defined as a mutually beneficial *external* partnership between two organisms of different kinds, as in the association of certain hermit-crabs with certain sea-anemones.

(9) Symbiosis is more intricate—a mutually beneficial *internal* partnership between two organisms of different kinds. It may be between a plant and a plant, as in lichens; or between a plant and an animal, as in the green freshwater sponges, with their unicellular Algæ; or between an animal and an animal, as in the beautiful Infusorians that help digestion in the food-canal of wood-eating white-ants.

(10) Then there is the large assemblage of parasites, at various grades, such as ectoparasites and endoparasites, and including almost incredible phases, such as the organic continuity between certain pigmy male Angler-fishes, and their more vigorous mates.

(11) Perhaps to be regarded as instances of discontinuous commensalism are such partnerships as that between certain ants and their associated Aphids with abundant honey-dew, or that between other ants and minute guest-beetles, sometimes with attractive exudations.

(12) The series naturally ends in gregarious and social associations whose members are of the same kith and kin—in flock and pack, in termitary, ant-hill, and beehive, in rookery and beaver village.

The analysis given shows the complexity of inter-relations between organisms, and yet it is far from complete. It requires a large addendum of "Miscellaneous Linkages".

SOCIAL ANIMALS

1. A thousand passengers on a liner make an isolated aggregate of individuals, but they do not constitute a society. Yet if they were wrecked on an uninhabited oceanic island, they would soon strike the social note. That is to say, they would begin to show corporate action. They would begin to act as a unity, as a whole which is more than the sum of its parts. Similarly with animals, there is nothing social in the multitude of mites in the cavern of a cheese, but even a small community of ants is a societary form. Hard-and-fast lines are impossible; aggregate shades into integrate; but there is no mistaking even a feeble social note which is sounded whenever a group of individuals begins to act as a whole, with some self-subordination among the members. There may be a thousand barnacles hanging from a floating log, but there is not in the whole quaint company the slightest hint of the social. Yet beginnings are perceptible when a troop of cuttle-fishes swim together harmoniously, keeping together in one direction, flushing with colour-change at the same instant. The simplest expression of the social is when a number of normally solitary animals migrate together, as if moved by a common spirit. A mass-movement of starving lemmings or of still wingless locusts may be at no higher level than the disorderly flight from a burning city, but a migration of reindeer or a march of driver-ants is definitely social.

2. A further step in the evolution of social life among animals is illustrated by troops of monkeys, which sometimes combine to raid an orchard; and yet more by the members of a beaver "village", who unite to dig a canal through an island in a river; by a herd of elephants, which can combine into a formidable charge; by the winter pack of wolves, who hunt individualistically in the summer time, or, in its way best of all, by the prairie-dog-like viscachas of La Plata, that may even arrange an expedition to unearth an adjacent colony whose burrows have been closed by the farmer.

Many other instances may occur to the student, but one must emphasise the point that mere gregariousness is not in itself social; there must be evidence of some corporate activity. A herd of cud-chewing herbivores strikes the social note when there is anything like combining against a carnivorous enemy, or posting sentinels, or setting off on a journey with one accord.

Among the social birds a prominent place must be given to the rooks, the cranes, and the parrots—all of them big-brained. Large numbers of sea-birds, such as gannets and guillemots, often nest together, but this may be mainly because there are not very many suitable cliffs with nesting-ledges. Thus there are not in the world as many as twenty breeding-places of gannets. But in these crowded haunts there is almost no hint of sociality, except that the excited throng, flying out when disturbed, must automatically serve as a deterrent to predatory intruders such as falcons. And yet among those birds that nest gregariously, such as cliff-swallows, the social note is definitely struck when there is an organised, if not deliberate, mobbing of birds of prey that dare to come near. From such simple beginnings there is an inclined plane to the rookery, where concerted action is common, and conventions are unmistakable. There seems to be no doubt that pelicans sometimes make themselves into a living seine-net, wading in a semicircle towards the shore and driving the fishes before them. This successful first step in corporate action may be contrasted with the behaviour of herons, which always keep themselves to themselves in their fishing, though we occasionally see half a dozen at short intervals in a row. They are, of course, gregarious in their nesting, and show some unanimity in their routine through a long summer day. But the heronry is far below the rookery as a social formation.

But while there are well-known social mammals and social birds, such as those above referred to, it must be admitted that sociality is hard to find among reptiles, amphibians, and fishes. Perhaps this is an indication that a certain fineness of brain and mind is a pre-condition of social life. Perhaps it merely means that the need for social combination has not become urgent at these lower Vertebrate levels; and yet there are many reptiles, amphibians and fishes which have a very hard struggle for existence, and cannot find it easy to keep their place in the sun. One would welcome even a secret society among the New Zealand Sphenodons and other "living fossils" if that would keep them from disappearing.

No doubt there may be hundreds of frogs in a marsh or even on a tree, and there seems a hint of communal singing in their serenading, though it sounds cacophonous to our refined ears; but that is, we think, the nearest approach to sociality in amphibians. There are places, in the Dalmatian Islands, for instance, where it is difficult to pick one's steps among the welter of lizards, whose

contemporary evolution was studied so brilliantly by the lamented Prof. Kammerer, but dense crowding is not in itself social. No evolutionist expects to find hard-and-fast lines, and we are far from asserting that birds are the first Vertebrates to sound the social note. We simply wish to make it clear that the occurrence of, say, shoals of mackerel, whiting, sprats, or herring does not illustrate sociality. Yet we are interested when a recognised ichthyological authority, Dr. Harry M. Kyle, says in his *Biology of Fishes* (1926) that the smaller kinds sometimes *combine* to attack the larger. For that sounds, however feebly, the social note. "The salmon is

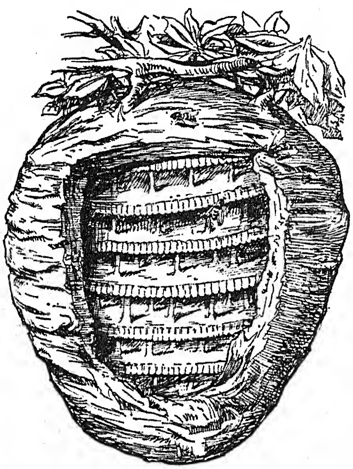


FIG. 30.

A Wasp's Nest. From a specimen. The structure is made of chewed wood, which may be compared to paper. One storey is fastened to another, and each bears down-turned cells in which the eggs develop into grubs. The series of combs is surrounded by windproof and waterproof envelopes.

one of the most powerful fishes in fresh water, yet the much smaller eels have been known to work together to devour it, even in the pride of its strength before spawning." Perhaps it is just as well that there are not more than adumbrations of social combination among the low-brained reptiles, amphibians, and fishes. Vain man would not like to hear of the Honourable Company of Cobras or the Union of Operative Sharks!

3. Among Backboneless Animals there is notable sociality in almost all the ants, in all the termites, in 500 out of 10,000 species of bees, in many of the wasps, and in a considerable number of beetles. Of crowded gregarious life without corporate action there are many examples, as in shoals of "sea-butterflies" (open-sea molluscs), great companies of free-swimming crustaceans and sedentary acorn-

shells, clouds of midges and Mayflies, vast groves of corals and zoophytes. The variety of form and habit is so great that it is not surprising to find every here and there some social activity. Thus the social note is struck when the Procession Caterpillars go on the march in Indian file, the head of one touching the tail of its neighbour in front. This makes for efficiency when the leader finds a patch of moist soil into which they all burrow and undergo metamorphosis; and it is no argument against the general efficiency that the file should continue for days in futile circumambulation, as when Fabre led the procession round his fountain edge, the head of the leader touching the tail of the hindmost. It is characteristic of instinctive behaviour that it loses its effectiveness when there is a departure

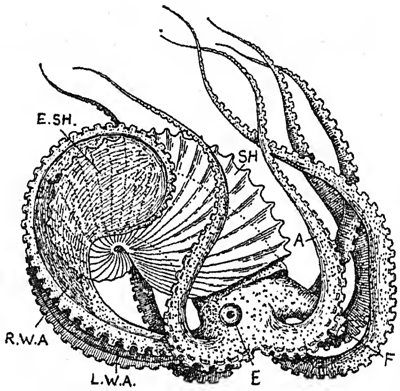


FIG. 31.

Female Paper Nautilus in its Swimming Position. A, one of the ordinary arms; SH, exposed portion of the shell; ESH, enveloped portion of the shell; RWA, right webbed shell-making arm; LWA, left webbed shell-making arm; E, eye; F, funnel. From a specimen, contradicting most figures.

from the ordinary routine. But our present point is that the march of the Procession Caterpillars is a social beginning, and so also for the common canopy of silk with which they invest themselves when they are browsing on the branches of the pine-trees.

One of the most beautiful sights in the world, sometimes seen in the Mediterranean, is a fleet of female Paper Nautili or Argonauts. Each is seated in a delicate spiral shell, more of a cradle than a house, and, looking backwards, each is driving itself forwards by an outgush of water through a narrow funnel opening out of the gill-chamber. They sometimes move slowly in long lines on the surface of the sea, but that in itself is not more than gregariousness. The slender social beginning is in the fact that one Argonaut is sometimes linked to its neighbour in front by having one of its arms resting on the other's shell, while it is itself in turn touched by a neighbour from behind.

4. Here it may be appropriate to link social animals to those that form colonies physically continuous. Just as in the physical world, where electrons and protons combine to form atoms, and atoms molecules, and molecules micellæ in a colloidal state, so in the realm of organisms there are somewhat similar groupings, and regroupings even to colonies. Among the unicellular Protozoa a colony may be formed by continuous budding or by the cohesion of units as they divide. These colonies, e.g. among Radiolarians and Infusorians, are interesting in pointing the way to the origin of a multicellular body. In the beautiful green colony called Volvox, there may be as many as 10,000 cells, forming a hollow ball, and united to one another by delicate protoplasmic bridges. Each cell has two flagella

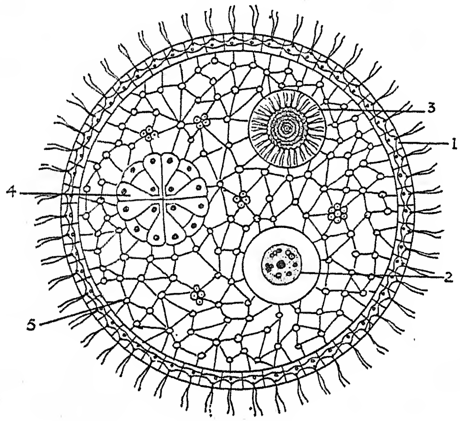


FIG. 32.

Hermaphrodite Colony of Volvox. Covering the surface are hundreds of bi-flagellate units (1) and (5); 2, an egg-cell; 3, a ball of male elements or spermatozoa; 4, a fertilised egg-cell segmenting to form a ball of cells, a daughter colony. After Klein.

and a directive eye-spot, and the colony swims in a spiral as if it were a single cell. An aggregate has become an integrate.

Animals that feed easily and abundantly on micro-organisms or on organic debris in the water tend to have more income than expenditure; and this naturally leads to growth. When the nutritional superfluity is intermittent rather than constant, the formation of new individuals by budding is more likely to occur than the great enlargement of a single individual. Moreover, the formation of a colony by budding opens up the possibility of arborescence, a very profitable mode of growth, which finds its climax in some of the immense "sea-fans" and "sea-pens", where thousands of individuals live in physical continuity, yet without undue crowding. A third advantage of colony-forming is seen when there is division of labour

and associated polymorphism—different castes of individuals in the colony working each in its own way, yet for the common good. Thus in hundreds of different kinds of Alcyonarians and Pennatulids there is dimorphism, minute siphonozooids keeping up a current throughout the colony, while the larger autozooids look after

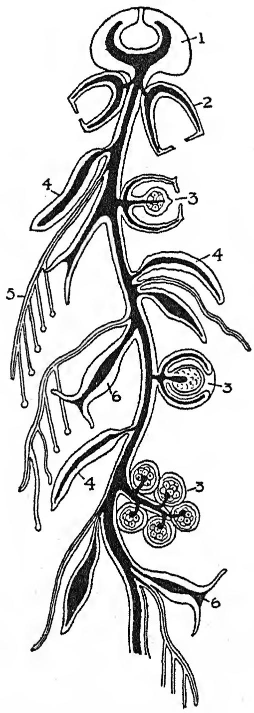


FIG. 33.

Diagram showing the Division of Labour in a Siphonophore Colony, related to the Portuguese Man-of-War. After Lang. 1, An individual modified into a float; 2, an individual specialised for swimming; 3, an individual showing the beginning of reproductive cells; 4, an individual modified into a bract-like protective sheath; 5, an individual modified into a long tentacle, bearing many stinging cells; 6, an ordinary nutritive, polyp-like individual.

nutrition and effect reproduction. In some of the hydroid colonies, such as the Hydractinia which covers the borrowed whelk shells tenanted by hermit-crabs, the division of labour results in nutritive, reproductive, sensory, and perhaps defensive types of individual. In the free-swimming Siphonophores, such as the Portuguese Man-of-War, the polymorphism or division of labour in the colony reaches its climax, for there may be as many as half a dozen different kinds of individuals. This should be compared with the diversity

of types that may be found in a true society of many individuals, such as a community of white ants, of which Maeterlinck has written so interpretatively.

The formation of colonies finds very varied expression among the Cœlentera (all or mostly stinging animals), such as zoophytes, Siphonophores, and sea-pens; but it recurs at a higher level in the Polyzoa or Bryozoa, where again there may be remarkable division of labour. It is seen also in a remarkable type called Cephalodiscus, which lies near the border-line between Invertebrates and Vertebrates. In this type the individuals composing the colony are not connected to one another save by a common investment; yet in the possibly related Rhabdopleura, another very remarkable animal, the individuals are united by a common stolon. The highest reach of such united colony-formation is found among the Tunicates, and while the majority are fixed and often beautifully grouped, there are some free-swimming types, such as the brilliantly luminescent "Fire-flame" or Pyrosome, which may be as long as one's arm. In many of these "social" Tunicate groupings the individuals (formed by budding) have separate inhalant orifices but share an exhalant orifice with a group of neighbours, or, as in the Pyrosome, with all the members of the colony.

The gradations in animal colonies are instructive. (1) A complex sponge may be formed by the fusion of numerous budded individuals, but it is rather an imperfectly integrated body than a colony. The individuals lose their distinctness and coalesce. The various parts or regions of the big body do not always work together in harmonious interdependence. A large portion may be cut off without making any difference. A living bath sponge may be cut up and bedded out. In fact, there is practically no division of labour, and there is no trace of a nervous system, not even of nerve-cells. (2) A level not much higher is represented by the huge masses of "brain-coral" and some of the other reef-builders. There may be indistinct delimitation between adjacent polyps, which arise by budding or by fission. Thus one polyp may produce another with a separate mouth, tentacles, and gullet, but sharing a common gastric cavity. But nerve impulses can pass from one part of the colony to another by networks of nerve-cells. Integration is beginning. (3) In most Alcyonarian corals each member of the colony is complete in itself, but all are connected by canals, and it is characteristic of the Alcyonarians, as contrasted with reef-building Madrepores, that a new individual is not directly budded off from an older one, but arises indirectly from a canal or stolon. (4) Slightly higher on this inclined plane are the dimorphic Alcyonarian colonies. (5) Worthy of a separate level are some of the Pennatulids or sea-pens which can move as a whole. They are not fixed to the substratum, but have their basal end freely embedded in the mud, and they are able to

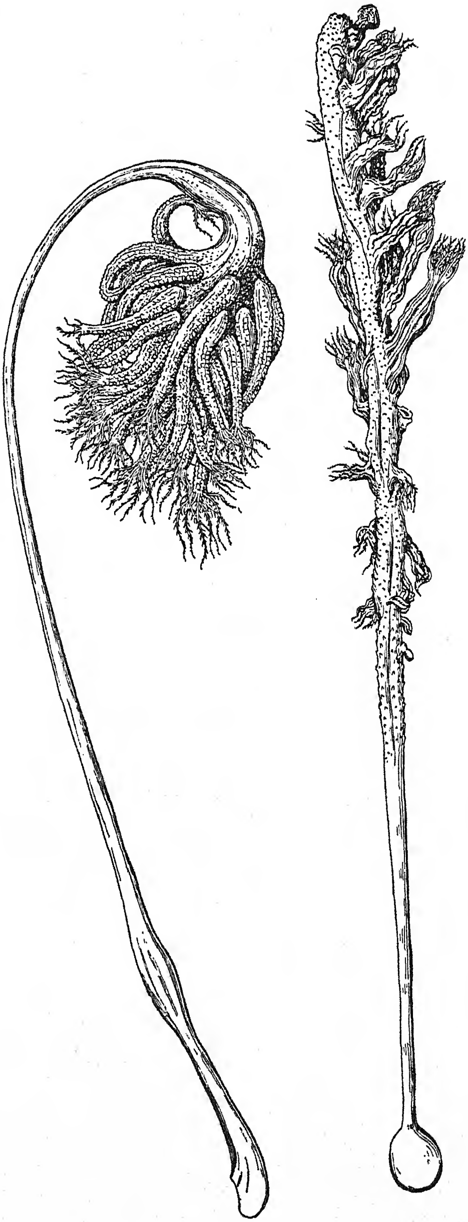


FIG. 34.

Two Deep-water Pennatulid Colonies, adapted by the long stalk to lifting the polyps above the smothering ooze in which the basal part is embedded. From specimens. Umbellula, to the left, has an apical tuft of polyps, more or less pendent at the tip of a stalk which may be over a yard in length in large species. The other colony, Stachyptilum, is more or less rigid, and bears its polyps in a less concentrated series.

retract forcibly. Thus in his *Naturalist's Voyage*, Darwin wrote of Stylatula: "At low water, hundreds of these zoophytes might be seen projecting like stubble, with the truncate end upwards, a few inches above the surface of the muddy sand. When touched or pulled they suddenly drew themselves in with force so as nearly or quite to disappear." (6) A higher level has been reached by many of the simpler free-swimming Siphonophores, such as the beautiful bluish Velella, fleets of which are sometimes seen in the Mediterranean, each with a vertical triangular sail rising above the surface. Here and elsewhere there is division of labour and unified locomotion. The "Fire-Flame" Tunicate illustrates the same level of integrated locomotion. (7) Highest of all and very striking are the most complicated Siphonophores with hundreds of polymorphic individuals, yet so well integrated by their nervous system that the colony swims as if it were a slow-going fish. It is a remarkable Natural History fact that a Portuguese Man-of-War, a group-unity of many small members, can capture a mackerel that comes against it. But our general point is simply that animal colonies illustrate a gradual inclined plane from aggregates to integrates.

5. One line of integrative evolution ends in free-swimming colonies such as the Portuguese Man-of-War and the Pyrosome. A second line is that of the instinctive societies that find a climax in the ant-hill, the beehive, and the termitary. They obviously differ from the colonies we have discussed in being physically discontinuous. The bonds are psychical rather than physiological, but they vary greatly in their subtlety. It is a noteworthy fact, vouched for by that skilled observer, Wheeler, that social habits have arisen among insects no fewer than twenty-four different times; and this number will probably be added to as our knowledge of tropical insects grows. This fact is enough of itself to indicate the strength of the organic trend towards co-operation or sociality. But there are many diverse societary forms: "some of them are small and depauperate, mere rudiments of societies, some are extremely populous and present great differentiation and specialisation of their members, whereas others show intermediate conditions." Our first question must be in regard to their common features.

(*a*) A society of termites may include many thousands of individuals, but they are all descended from a pair of "founders". This is the typical state of affairs among social insects, though there are some large ant-hills that include several queens, each with her own abundant progeny. In the transient summer colony of the Humble-bees some of the workers may lay eggs, which, being unfertilised, develop into drones, so that for a short time there are three generations together; and this may occur elsewhere. But the typical community among ants, bees, and wasps consists of a queen and a large body of offspring; the great majority being arrested females or

workers, and a minority being males or drones. One of the peculiarities of the termitary is that the workers are reproductively arrested individuals of both sexes.

(*b*) A second common feature is the prolongation of the mother's life. In many insects reproduction is fatal, as is often seen in the death of delicate butterflies soon after pairing and egg-laying. As is well known, the Mayflies, which may have a larval aquatic life of several years, may have their winged, aërial, reproductive life reduced to a single evening. In one species of these Ephemerids the adult life is said to be condensed into a single hour! It is plain enough that it would be difficult for the social habit to be established under such conditions, for it implies a prolonged maternity and the coexistence of numerous individuals of different ages. In most cases there must be nurses to look after the relays of larvæ.

It is a familiar, but none the less remarkable, fact that in the

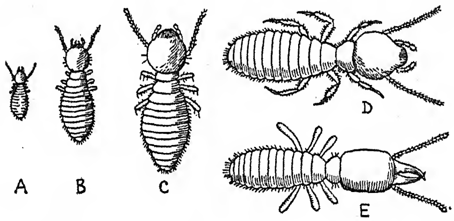


FIG. 35.

Different Forms of Termite. A, Young larva; B, adult worker; C, young queen; D and E, two types of soldier. After Escherich.

majority of insects the mother never sees her offspring. Under a stone we may find a mother earwig with her miniature young ones running about beside her, forming a family, but this is an unusual scene. In most cases the mother has died before the young ones emerge as winged insects, if not as larvæ. Thus the usual brevity of the mother's life among solitary insects precludes the social habit, though there may be elaborate exhibitions of instinctive maternal care in the provision of the nest with food for the emerging larvæ. The evolution of the social habit implies not only an increase in maternal care, but an evasion of the Nemesis of death after reproduction. In starting a community the mother, as in the familiar case of the Humble-bee, must be the first nurse. It is only later that she can devolve her duties on her senior offspring. As Wheeler insists, it was the lengthening out of the maternal stage that made social life possible. Societies, among insects at least, are based not only on maternal devotion, but on maternal vigour. Everything depends on the mother being strong enough to be a nurse, and strong enough to have repeated periods of egg-laying.

(*c*) Among the other general features of the instinctive society is the widespread division of labour which occurs at all grades. In the six unrelated families of social beetles there is, as Wheeler has shown in detail, no division of labour except that between males and females; and in some types the males are almost as devotedly parental as their mates. At the other extreme are some of the termite societies which have eight different castes, each represented by dimorphic sexes, giving a total of sixteen different forms. The division of labour has, of course, reference to the two perennial problems of hunger and love, or nutrition and reproduction; and what is attained in instinctive societies by variational and modificational polymorphism is secured in intelligent societies, such as the beaver village, the winter wolf-pack, and the troop of monkeys, by intelligent devices. There are many quaint details in the solution of the nutritive and reproductive problems. Thus, as regards nutrition, many wasps illustrate a curious process which Roubaud calls "oecotrophobiosis" and Wheeler "trophallaxis". When the mother in the case of solitary wasps, and the worker in the case of social wasps, is transferring to the grub some pabulum such as a chewed insect, she receives in return a drop of elixir which is secreted from the enlarged salivary glands of the larva. It means so much to the workers, as a douceur for their industry, that Roubaud goes the length of regarding the attainment of the luxury as a factor in the elaboration of the society. Then, as regards reproductive details, what could be quainter than the reserve "kings" and "queens" among the termites, castes of complementary reproductive individuals which can be utilised in replacing the functional royal pair if need arises?

To these two general features of prolonged reproductivity and division of labour (giving place to what are surely nearer intelligent devices and plasticity), there may be added a sensitiveness in kin-recognition, and also a readiness, especially in instinctive societies, to be of assistance to those of the same community. Thus it is the rule in the ant community that an individual with food *must* feed the hungry on demand. In many cases, again, there is some particular organismal quality which gives the societary type an advantage over individualist rivals. Thus ants have their poisonous formic acid; bees have their wax; termites have in their food-canal an indispensable and invaluable contingent of partner Infusorians which make the wood-dust food more available. So, at higher levels, the rooks and the monkeys are more effective in their sociality because of their large vocabulary of significant calls. According to von Frisch, the success of a beehive depends to some extent on the bee-language, which takes the form of a quick excited dance on the honeycomb, exhibited by the worker-bee when she returns to the hive after finding rich treasure of nectar or of pollen. And the finesse of

Animate Nature is illustrated by the fact that the post-nectar-dance differs in some features from the post-pollen-dance.

6. It is interesting to inquire in detail into the advantages of the social or corporate way of living. It is interesting from the ecological or Natural History point of view, for the advantages illumine such achievements as the firmly built termitary, six feet high, with its many rooms and passages, the possibility of such undertakings as the beavers' dam, and the intricacy of the inter-relations between ants and other forms of life—both plants and animals. The inquiry into advantages is also interesting biologically, for it reveals the multitude of ways in which variations from the solitary mode of life towards the social might be seized upon and utilised by natural selection. And thirdly, the inquiry is interesting because it is suggestive in relation to human affairs. Animate Nature has been for hundreds of millions of years a vast experimental laboratory, whose results are at times for our warning, yet also, it may be, for our inspiration. No one proposes to argue from pismires to parliaments, or from mice to men, but he who runs may read from the study of social animals that for certain ends the co-operative or communal way of living is likely to be more successful than that which adheres to the "each for himself" policy. And with advantages there go dangers, to be separately discussed, which are luridly illustrated by the seamy side of the much admired, and in many ways most admirable beehive and ant-hill. Let us consider, then, in some detail, how the social habit has justified itself in the struggle for existence.

(I) The most obvious advantage of the social habit is in the strength that union gives. Individually, the ant is contemptible, but a raid of driver-ants may be a terror; and the harm done within recent years in Madeira by the invasion of the Argentine ant gives a striking diagram of the practical results of such concerted action. Small animals gain safety in combination; thus the fact that the small sand-martins are but little molested is partly explained by their large numbers. Birds that are individually insignificant may combine to "mob" a hawk, or an owl, or a cuckoo. Kropotkin pointed out long ago in his *Mutual Aid* that a small monkey has no chance against an eagle; yet the assailant bird may come off badly when the monkey's cries bring its comrades to its aid. There are, of course, many gradations between the sheer force of numbers and a unanimous combination in attacking or repulsing an intruding enemy.

(II) Slightly different is the increase in efficiency which is sometimes attained by combined effort. A familiar instance is the co-operation of several ants in the transport of booty, such as a big spider, which an individual cannot do more than move. A common sight in some tropical countries is the combination of eight or more tailor-ants in drawing two leaves together to form the beginning of

a nest. Very striking is the way in which they bridge a gap by forming, like gymnasts, a living chain, A being held in the jaws of B, who in turn is gripped by C. Even quainter is the way in which the two leaves, held close together by several members of the work-party, are fixed by others by means of glutinous threads, these being the sticky secretion of the larvæ, held in the mouths of the workers, and literally used as animated gum-bottles. There is no doubt that sociality may greatly increase efficiency. The fact that wolves hunt solitarily in summer, but in packs in winter, is probably in part a reaction to the scarcity of food in the cold months, a scarcity which makes combined tactics more effective. Of the same nature is the co-operative fishing seen in pelicans; and the like may have aided the more organised co-operation in the geotechnic labours of beavers.

(III) Of great advantage is the realisation of something in the way of permanent products, such as a termitary, an ant-hill, a beaver-dam, in which we see an adumbration of the external heritage, or social environment, which has meant so much to mankind. When there is an elaborate ant-hill or a beehive, the young animals have a basis on which to work, an objective registration of racial gains. Anything of this sort must serve as a liberating stimulus to inborn instinctive promptings, and must also promote the beginning of tradition. In the nests of wasps there is nothing that lasts; the sole survivors of the autumnal debacle are the young queens, who start a fresh nest the following summer. But it is different in an ant-hill, which continues from year to year, becoming, like a city, more and more elaborate. Something analogous to a tradition will more readily arise when relays of different ages are living together at the same time. It must be kept in mind that young animals may well be in some measure educated by a socially constructed environment that lasts, as in the case of a beaver-village, or even in a rookery that is re-established each successive year in the same group of trees. Apart from constructed external products, such as a honeycomb, there is also an educative potency in the framework of the society itself. For a young worker hive-bee, emerging from a brood-cell, finds itself in a busy organised world, in which the rôle it has to play is predetermined in remarkable detail.

(IV) A solitary insurgent animal, that has refused to enter any of the open doors to easygoing life, such as those labelled parasitism, commensalism, and symbiosis, must remain all-round in its development and activities; and this independent all-roundness claims our admiration. But a society, like a colony, makes division of labour possible; and this makes for greater efficiency in achievement and for greater economy of energy. Among leaf-cutting ants, so well described by Beebe, there are the usual females, males, and workers. But the workers may be divided into the productive and the militant

types. And the non-militant members, workers in the more literal sense, have diverse functions to fulfil. There are the foragers who cut off segments of leaf from the trees and carry them back to the underground city. Another function is the chewing of the leaves into a green paste, on which is grown a fungus, the sole food beneath the ground. A third function is looking after the young stages. The variety of function among non-reproductive ants is often associated with polymorphism of structure. Wheeler points out that they can be arranged in a graduated series, beginning with large and huge-headed individuals, more like the queen in stature, and ending with minute small-headed individuals, which may be almost like dwarf species. In Carebara, for instance, the worker may be a thousand times smaller than the queen! The largest of the worker types may serve as soldiers or policemen, yet their powerful jaws may have a pacific function—primarily, secondarily, or both, who shall say—for they may be used to crack seeds and hard parts of insects, "so that the softer parts may be exposed and eaten by the smaller individuals". These may be foragers, nurses, cultivators, sappers and miners, and so forth. Now it happens in some species that only the maximæ (the soldiers) and the minimæ (the ordinary workers) are left, the intermediate grades being eliminated. "In still other genera, where soldiers were not needed, or were too expensive to rear and maintain, on account of their great size and appetites, they too have been eliminated and the worker caste is represented only by the tiniest individuals of the originally polymorphic series."

Very quaint is the picture Bates gave in his *Naturalist on the Amazons* of the Saüba or Umbrella Ant of Brazil. The hard destructive work of cutting discs from the leaves of certain trees is done by workers with relatively small heads. Others, called "worker-majors", with huge heads, walk about looking on, without very obvious functions. They are not aggressive soldiers, and the foragers do not require foremen. "I think", Bates says, "that they serve, in some sort, as passive instruments of protection to the real workers. Their enormously large, hard, and indestructible heads may be of use in protecting these against the attacks of insectivorous animals. They would be, on this view, a kind of *pièces de résistance*, serving as a foil against onslaughts made on the main body of workers." But there is a third type, represented by very strange fellows, with the same kind of head as the "worker-majors", but "the front is clothed with hairs instead of being polished, and they have in the middle of the forehead a twin simple eye", which none of the others possess. But these must serve as instances of the polymorphism and division of labour among true ants.

Among termites (misnamed white ants) each non-reproductive caste consists of individuals of both sexes, almost or quite indistinguishable externally; and in the great majority of species there

are five castes altogether. First, there are the ordinary "kings" and "queens", the males and females, deeply pigmented, big-brained, with large compound eyes, and with well-developed wings which fall off after the mating. Second, there are complemental or substitutionary kings and queens, less pigmented and less well equipped than the first type, and with only traces of wings. Third, there are "ergatoid" complemental kings and queens, small-brained, scarcely pigmented, entirely wingless, practically blind, and dwarfish in size. Fourthly, there are the workers, unpigmented, wingless, small-brained, and quite sterile. Fifthly, there are the soldiers, big-headed, small-brained, wingless, with large jaws worked by powerful muscles. In some genera the mandibulate soldiers are represented by small individuals with retort-shaped heads, and with the opening of a large gland at the end of the long, tubular snout. These "nasuti", as they are well called, attack aliens by thrusting their snouts on them and squirting out a jet of colourless secretion which seems to act like glue, binding together the weapons or appendages of the enemy. This is one of the quaintest of the polymorphic types, whose origin is so puzzling. For how does one mother come to have five or more different types of offspring?

Before we leave division of labour and its advantages, we must notice the profitable arrangement which often secures a succession of functions in the course of the individual life. This may be illustrated by a reference to the recent work of Rösch on the apprenticeship, so to speak, of the hive-bee. By marking individual workers in an observation hive, Rösch was able to follow their gradual promotion from one kind of task to another in the course of their short life of a month or six weeks. The young workers, that have just emerged from the pupa stage, are first turned to the task of preparing and cleaning wax cells in which the queen will lay eggs. After a few days they pass, or are promoted, to the status of nurses, watching over the young bees in their cells. To begin with, they tend only the older larvæ, supplying them with pollen and honey, but later they are trusted with the younger stages, which require a nutritious fluid secreted by the worker-bee from glands that begin to function at this time, about the tenth day of adult life. When the worker is a fortnight old, more or less, she leaves her nursing work to spend a week in the general service of the hive, cleaning away refuse, distributing and storing food, and so on. Trial flights in the open may also be made, but on these first attempts no pollen or nectar is collected. Finally, at the age of three weeks, each worker undertakes the last of its indoor tasks, that of acting as a guard at the door of the hive, preventing the entry of strange bees or other intruders. When relieved from this duty, the worker-bee devotes all its remaining life and strength to the arduous work of collecting nectar and pollen from the flowers. Here, too, there may be division of labour, for the

bee does not flit erratically from flower to flower, but shows herself, as Darwin said, "a good botanist". Once settled down to tapping a profitable and abundant species, she may keep to this for the whole of her outdoor life—perhaps three weeks—without ever entering another kind of blossom. Rösch's study is interesting in proving a regular succession of functions, an obviously profitable arrangement when there is a continuous sequence of fresh offspring. The study is also of interest in correcting the impression one is apt to get of the tyranny of instinct. We suppose that it is partly by a developmental sequence of instincts, and partly by hive-conventions, that the worker-bee is prompted to one kind of activity after another.

(V) A fifth advantage of the social habit is that it fosters the evolution of intelligence in the big-brained types and of instinctive efficiency in the small-brained types. As the evolution of instinctive behaviour remains very puzzling, we shall confine ourselves mainly to instances of intelligence. In regard to instinctive behaviour, the Lamarckian view refers it to a racial entailment of the individually enregistered results of tentatives and experiments, while the Darwinian view starts from germinal variations in the nervous system, which are tested in the individual's unceasing experimental initiatives, and are thus subjected to natural selection. In both cases the change in the nervous system may be supposed to be correlated with some psychical change, for there are many instances of instinctive behaviour of which it is difficult to make sense if we persist in regarding them as no more than chains of reflex actions. In many cases it seems legitimate to suppose that the instinctive behaviour is backed by purposive endeavour and suffused with awareness, often accompanied by feeling. But the important consideration here is this, that an incipient social organisation, on the instinctive line of evolution, will, *ipso facto*, afford suitable sieves for winnowing new variations of the same general nature.

Perhaps the case is clearer when we deal with societies on an intelligent basis, i.e. with evidence of individual inferential learning. Our proposition is that social inter-relations would favour the advance of intelligence. This is suggested when we mention monkeys, beavers, wolves, and wild horses among mammals, or rooks, cranes, and parrots among birds. The names suggest some correlation between nimble brains and the social habit. It may be objected, however, that this is arguing in a circle. With one breath we say that a certain fineness of brain is a precondition of sociality, and then with another we say that societies make animals clever. But we believe that it is just in these virtuous circles that evolution has worked. Well-endowed animals with kin-sympathy and keen wits form an incipient society, but the social framework acts as a sieve in which further variations in the direction of increased sociality

tend to be preserved, while variations in the direction of the anti-social tend to be sifted out. To take a concrete case, the evolution of speech, there is no doubt that the first use of the voice was as a sex-call, and that it began among Amphibians long ago. Now while many solitary animals have a voice, it has obviously greater survival value in a society, where significant calls and cries are of more frequent usefulness. Thus a simple animal society in certain conditions would not only act as a stimulus to using sounds, but would tend to winnow out the variants with the more ineffective vocabulary. But this is not in the least at variance with the complementary idea that the acquisition of audible means of communication would favour the development of individual intelligence and the survival of the better-brained variants who used the new instrument to best advantage. "Nothing succeeds like success"; and evolution works on a subtle compound interest principle. Our proposition is that the social habit favours the advance of intelligence, both in the individual and in the race.

(VI) A sixth advantage of the social habit is that it works in what amounts practically to a moral and ethical direction. Many a solitary animal of predatory habits and each-for-himself ways is a pattern of parental care. Thus there is no surpassing that of the mother otter or the mother stoat. With admirable devotion they illustrate the maternal virtues, giving expression to their intrinsically fine natures. This "finish" of the maternal care is not surprising when we think of the survival value of education in these predatory and Ishmaelitish types. Thus it is plain enough that the social habit cannot improve on the parental care which is exhibited by many of the solitaries. At the same time it may be claimed for animal societies that they tend to foster kindly feelings. They presuppose a measure of kin-sympathy; the complexity of inter-relations stimulates social feeling in the individual; and the welfare of the society demands the winnowing out or elimination of variations in an anti-social direction. Thus animal societies have tended to favour what may be called the very materials of morality.

But they also adumbrate what is in a stricter sense ethical conduct, inasmuch as they demand a certain degree of self-subordination, and a measure of willingness to recognise the claims of others. The social animal at this intelligent level, as we must so far call it, has to habituate itself to work in a team; and is it not one of the deepest of moral lessons to learn to "play the game"? Moreover, in the animal society there is the beginning of conventions and unwritten laws; there is sometimes, as in the rookery or the wolf-pack, a powerful social restraint on individual impulse. This points towards ethics.

(VII) There is, we think, a seventh great advantage in the social way of living, that it allows of the trial of variations with a freedom

that is rarely possible under the each-for-himself régime. The existence of a society that has even the beginning of success serves automatically as a shield for variations that might arise, but could not possibly continue in the conditions of individualistic life. There are oddities and whimsicalities among social animals that are hardly conceivable under non-social conditions. Thus the soldier termites have very strong mandibles which are useful in the fray, but make it impossible for their possessors to chew the wood which forms the dry-as-dust diet of these spartan insects. So the soldiers have to be fed by the workers. Among the so-called Honey-ants of Texas and Colorado, which usually frequent places with prolonged periods of drought, there is a well-known and indescribably quaint custom of storing honey-dew. The foragers are unable to make receptacles of any sort, so they discharge their drops of dew into the mouth and crop of some of their stay-at-home fellows. The crop becomes so much dilated with the honey-dew that the abdomen becomes tense and spherical like a yellow currant. These individuals, called "repletes", who "assume the rôle of animated demijohns or carboys, are quite unable to walk, and therefore suspend themselves by their claws from the ceilings of the nest chambers". When an ordinary worker is hungry it strokes the head of a replete and receives by regurgitation a droplet of the honey-dew collected in days of plenty. Only in a society could such an extraordinary specialisation exist.

7. Great advantages are usually taxed; great steps of progress are usually dogged by risks. Tennyson saw "Reversion ever dragging Evolution in the mud". So it is with the highly evolved social habit, both in animal and in man. The first risk is that of losing the independent all-roundness of the each-for-himself type. Self-subordination may go too far, and the division of labour may result in types that are not viable except under the ægis of the society. The big-jawed soldiers among the termites have to be fed from the surplus that the workers can afford. The animated honeypots that hang themselves up on the roof of the nest of the sweet-toothed ant of Texas are doubtless very useful, but though they are called "repletes" they cannot be said to live a full life. The big-eyed drones of the beehive have well-developed wings and wing-muscles, and are far from inactive. But they have no arrangement for collecting pollen; their tongue is very short; they have no wax-glands; and they are unable to collect food for themselves. They will thus starve rather than forage. We do not blame them for trading on their masculinity, any more than we would give them a minus mark for not having a sting, which, being a transformed ovipositor, is always confined to females; we are simply pointing out that they could not survive if they were not members of a community. They are danger-posts on the highway of sociality. In the same way the bloated

queen termite has almost become a fixed egg-producing machine, verging on the pathological.

One of the striking differences between civilised human society and Wild Nature, with which man has not interfered by crowding and over-preserving, is that disease is rife in the former and almost absent, apart from parasitism, in the latter. In Wild Nature it is difficult to find examples of occupational, environmental, constitutional, or even microbic disease, but it is noteworthy that some approaches to diseased conditions occur in animal societies. Both among ants and termites there are instances of guests or pets, usually small beetles or Diptera, to which hospitality is shown, usually because of certain exudations which are luxuries to the hosts. Now these guests or pets sometimes sink into a degraded condition called "physogastry". This means that the abdomen becomes bloated and what might be roughly called dropsical. The wings are lost, the eyes degenerate, the whole life becomes sluggish. According to Wheeler, the modifications seen in the physogastric guests of certain termites are directly referable to the stuffy, humid atmosphere of the termitary, the cramped dark passages, and to their over-abundant carbohydrate diet. But the important point is that the queen termite herself is an instance of a like physogastric state—she is a physiological martyr to exaggerated maternity in a servile state. This is an obviously suggestive illustration of the fact that a society may not only throw its shield over highly specialised types, who could not stand alone as isolated individuals, but may even shelter undesirable unhealthy types. This, as we know to our cost, also tends to arise in man's so far civilised societies.

In some instinctive societies, such as those of ants, bees, and termites, we get another glimpse of a seamy, almost sinister, side. The efficiency of the society may depend on arrangements which are repellent to human ideals. It would be a gross anthropomorphism to criticise these arrangements on that ground, for man's ethical and artistic criteria are not here relevant; yet the facts show that very effective social organisation is not necessarily entirely on the lines of what man calls progress—an ideal which we venture to define as including all movements towards health (i.e. a fuller life), and towards wealth (i.e. an increased and more economical mastery of Nature's energies), and all movements towards a diffused and heightened embodiment and enjoyment of the true, the beautiful, and the good. Now this human ideal has plainly to go far beyond the world of social animals.

A beehive displays a fine instance of wealth, perhaps the most beautiful form of wealth in the world, the honey in the honeycomb. There is also a fine display of health, for in spite of the Isle-of-Wight acarine disease, and some microbic maladies—for which man's greed and over-coddling may be responsible—there is outstanding

vigour and industry in the beehive. And on the whole, until we probe beneath the surface, the beehive, like the ant-hill or the termitary, shows a smooth-working, harmonious, well-integrated social life. Indeed, the social organisation of the hive is a marvel which angels might desire to look into. What then is wrong?

In the first place, the hive-bee community depends on a specialised reproductive female caste, the non-productive queens, who have a tongue too short to reach almost any floral nectary. They have no apparatus for collecting or carrying pollen, and as they have no wax-glands they could not make any honeycomb. Yet a ripe queen may lay three thousand eggs in a day, and she may continue egg-laying at the proper season for about three years. In the second place, there is the specialised caste of reproductive males or drones, wastefully numerous, mostly quite futile even in their masculinity, an expense to the community, and with a harsh, if not painful, ending. As long as food is abundant they are treated good-naturedly, but as the pinch of opening autumn begins to be felt, they are met somewhat grudgingly. More and more they get the cold shoulder; and if they do not take the broad hint to keep away from the hive, they are expelled by force. Some die by violence and others from the early frost. Only in rare cases, according to von Frisch, is there anything approaching the often-described massacre of the drones; but there is no doubt as to the grim reality of cold-shouldering.

In the third place, the whole economy of the hive rests on the vast multitude of arrested females, usually non-reproductive. They have better brains than the queens, but their brain-cells go steadily out of gear from over-fatigue; they are models of the virtues, but they are "Robots" wound up to over-industry. The shining hour does not improve the busy bee, for though summer-bees can live, as Dr. John Anderson has shown, for three months, they do not usually attain to more than four or six weeks.

8. When an attempt is made to envisage the evolution of the social habit in animals, it seems useful to distinguish as preconditions (*a*) some measure of kin-sympathy and sensitiveness in recognising kindred; (*b*) a certain fineness of nervous system, whether of the little-brain or big-brain type, which need not be thought of, especially among birds and mammals, without its psychical correlate; and (*c*) some considerable power of prolific reproduction, since a very small society is all but a contradiction in terms. Yet, as we have seen, the last precondition may be dispensed with when there is a seasonal combination of many families as in the pack of wolves, or a permanent combination as in rooks. To put it negatively, an animal society is not likely to arise among types of animals that are sensorily or emotionally indifferent to their kith and kin, or among types with a low type of nervous system and a dull mentality, or among types that do not occur

together in considerable numbers. Yet there may be a huge congregation, to return to the mites in the cheese, without any hint of sociality. A prettier picture may be found in the crowd of jellyfishes often seen slowly moving in a summer sea. They certainly form no fleet, as a school of dolphins may be said to do.

Negatively again, the formation of a society implies that the quest for food is of a type that allows of numerous co-operators, that the food is of such a nature that a large supply is available within an area relatively small in proportion to the means of locomotion and transport, and that storage is possible should the year include a season during which food is unprocurable.

9. If these conditions are fulfilled there are two main ways in which animal societies may arise. As already indicated, the evolution of the social habit on instinctive lines, as in ants, bees, and wasps, may be traced back to a lengthening out of the period of vigorous maternity, so that successive sets of offspring are produced in rapid sequence, among which division of labour—partly variational and partly modificational—may arise and prove a notable source of strength. On the other hand, among birds and mammals, that is to say in societies more intelligent than instinctive, the evolution is slightly different, for it implies the combination of several, it may be many, families. It is more likely to arise in circumstances where corporate or integrated action has obvious survival value; e.g. in concerted defence against enemies. It is assisted not only by division of labour, but by sounds, virtually words, and other social signals and symbols, by the traditional growth of conventions, and in some cases by the accumulation of permanent products. Yet when all is said, it seems clear that the social habit is only for the élite. There are only 500 species of social bees amidst a total of ten thousand, and the distinctively social mammals are in a small minority. If man appeals to the Animal World for corroboration or condemnation of his ways of living, what can the answer be save that the two policies—the each-for-himself or individualistic and the co-operative or socialistic—are both effective? Each has its advantages and its dangers. For certain ends the otter is to be imitated, and for other ends the beaver. The ecological judgment is not in favour of socialisation only or individualism only, it recommends both in judicious complementariness.

10. We cannot conclude our inquiry without a warning against that type of over-simplification which regards the study of human societies as part of the ecology of mammals. That is a "biologism", just as it is a materialism to insist that life is adequately describable in chemico-physical terms. It must be recognised that a human society stands high above all the integrates that we may study among the beasts of the field. Man has language, rising high above animal words; he commonly displays reason or the capacity for conceptual

inference, rising high above the intelligence or perceptual inference beyond which animals do not seem to attain; he has a more or less clear consciousness of his history, and he is evolving a social conscience; he has the power, if he would oftener exercise it, of guiding his conduct in reference to ideals, social as well as personal; he has apparently unlimited possibilities of ameliorating his social heritage and making it more available; in a new way he can in some measure control his own evolution. The story of social animals is interesting and suggestive, with many warnings and not without inspirations, but it is not as yet more than the first sketch of an introductory chapter to Human Sociology.

It is evident, however, that it would be great gain if we could begin to formulate some general conclusions in regard to animal anticipations of human societies. Great as the gulf is, there must be valuable suggestions from prehuman experiments in sociality. We all know scores of extraordinarily interesting facts in regard to ants, bees, wasps, termites, rookeries, beaver villages, herds and packs and troops; but are there any general conclusions? In many animal societies experiments have been made which take our breath away in their daring. Can we learn from them?

Thus there is the experiment of having a specialised reproductive caste, as in queen-bees and drones. There is the experiment of having individuals set apart to be reservoirs of the communal wealth, as in the bloated honey-ants that hang like small golden grapes from the rafters, to be tapped when the time comes. There is the experiment of eliminating the surplus population, as in the fatal cold-shouldering of the drone-bees as the season advances, and its gradual accentuation into an almost vicious use of the poisoned stiletto. There is the experiment some ants have made of keeping slaves, with the result that the gentry have become unable not only to forage, but to chew. There is the termite experiment of keeping up a military class, whose jaws, specialised for combat, are unable to masticate the dry-as-dust food of these strange ascetes. They have to be fed, not very daintily, by the workers. Most prominent of all is the beehive experiment of having an enormous proletariat of arrested females, obsessed by a mania for "work", for a self-subordinating industry which allows them a life of about six weeks or two months in summer.

SOCIAL ACTIVITIES.—In what forms of activity does the social life of animals find expression?

(*a*) There are corporate enterprises of many kinds, often subtly intermingled. It may be for defence, like wasps against an intruder, or soldier-termites against the assaults of true ants. It may be for attack, as when small birds "mob" a hawk or an owl. It may be in food-getting, as when pelicans wading in a half-circle close in upon

the fishes, or wolves in a pack surround their victim. It may be in making a communal shelter or store, as in termitary and honeycomb. It may be in the utilisation of other creatures, as some ants show with the Aphids which they milk, or leaf-cutters with the peculiar fungus which they cultivate. These concerted enterprises sometimes take subtle forms, as in the slave-making raids of the Amazon ants, in which established slaves may come to play the major part in the recruiting. Then there are the "wars" of some ants and the social plays of others. There is community singing among the howling monkeys. Also social in many cases is the assembling of migrants, and even such details as the wedge-formation, so familiar in wild geese, but seen in many other birds.

(*b*) In another group may be ranked a variety of activities in which the members of a society communicate with one another. Clearest, of course, is the use of sounds, simple kin-calls to begin with, but rising to the use of distinct "words" with specific meanings. But information or excitement may be broadcast by odours, as in the case of the "sting odour" and "queen odour" in hive-bees. A worker-bee that has found a treasure of nectar makes this known in the hive by her peculiar dance, and also by the odour of the flowers she has lately visited. In the antennary communications between ants there is probably a combination of tactile and olfactory stimuli. Many mammals have gestures as well as words.

(*c*) But the society expresses itself also in what may be called traditions, customs, conventions, and "folk-ways". These have a mental aspect in instincts and predispositions, with their attendant feelings, and an objective aspect in certain cases in the permanent products, such as the termitary-edifice, or in the embodied organisation of the society, such as its polymorphism, if that exists. Among ants the appeal of the hungry must be met; among bees the workers must ascend through a graduated apprenticeship; among chimpanzees a cry of protest arouses an uproar of indignation in the whole company. But it is a difficult task to formulate the laws of animal societies.

SUMMARY.—As we have indicated, there are diverse types of society among animals. Some communities of true ants are simply large families, the progeny of one queen, occasionally with grandchildren, which are produced parthenogenetically by the normally non-reproductive "workers". Each of the communities of the unrelated white ants, or termites, consists of one large family, the progeny of a pair, with the same occasional addition as before on the part of some female workers and soldiers. Among true ants all the workers are arrested females; among termites they are arrested females and males, but only the former are ever reproductive. In other communities of true ants there are several large families, each the progeny of

a particular queen, yet all working harmoniously as members of an integrated societary form. This shows that the difference between a large family and a small society is not of much importance from the sociological point of view. The essential features of a society are corporate action and some degree of self-subordination, which is sometimes, though by no means always, accompanied by division of labour, as in the case of the workers and soldiers already mentioned.

Animal societies may be usefully distinguished as predominantly intelligent and predominantly instinctive, with gradations between the two. Thus societies on a predominantly intelligent basis are illustrated by a troop of baboons, a herd of elephants, horses, or cattle, a beaver village, a community of prairie-dogs or of viscachas, while societies on a predominantly instinctive basis are illustrated by the communities among ants, bees, and wasps, and by the termitaries. Among social birds there is, no doubt, instinctive as well as intelligent behaviour; and among ants intelligent as well as instinctive, but the contrast between the two types is well marked. It is much more important than the distinction between societies composed of kindred of diverse descent and large families all children of the same mother.

Societies have evolved at so many different levels that it is difficult to define their preconditions. But there must be some capacity for kin-sympathy, and some fineness of brain. Mites and greenflies form great multitudes, but no societies. Yet there must be some degree of prolific multiplication, or else a long reproductive period in the case of slowly breeding animals like elephants. A small animal society is very rare; strength is in numbers. The mode of food-getting must be congruent with the social habit. Thus it is not surprising that there are among spiders only two or three social species. Interesting in this connection is the temporary assumption of sociality; thus wolves are solitary in summer and gregarious in winter, the very opposite of wasps!

As is usual with good things, there are seven virtues in sociality among animals. Many small and weak creatures become in their societies safe and strong, as ants well show. Operations impossible for a single individual are successfully organised, as when a number of ants drag large booty to the nest. There may be economisation of energy, as when one wild goose relieves another as leader of the flying phalanx. Economy is enhanced when there is division of labour, as in placing sentinels. There is an opportunity for forming permanent products, such as ant-hill and beehive and beaver-dam, which serve as what may be called an objective tradition. The social milieu is such that it fosters kin-sympathy and wits, sometimes rising to words, play, and artistic products.

The seventh advantage we must place by itself, it is so funda-

mental. A society always serves as a shield sheltering the individual in some measure from the external sifting, and allowing of the emergence and testing of variations and experiments which would have little chance in an entirely individualistic struggle for existence. This, as in human societies, sometimes leads to the survival of the biologically undesirable, sometimes verging on the pathological.

SYMBIOSIS

This rather fine word—symbiosis—which literally means living together, was first used in 1879 by the botanist De Bary to describe the partnership which he so much aided to demonstrate in lichens. For these curious plants, after long controversies before and after that time, have been conclusively shown to be not the distinctive group of cryptogamic plants they seemed, but a composite of others, a dual association of minute Algæ entangled in the meshes of a fungoid feltwork. The Algæ have chlorophyll and are therefore able to build up carbon compounds in photosynthesis like other green plants. In most lichens the partnership is very intimate, and, as one might say, perfect; but there are many gradations connecting these with somewhat rough-and-ready combinations. In most cases, however, there is no doubt that the symbiosis is mutually beneficial. The Alga utilises the water and salts which the fungus absorbs from the weathering surface of the rock or the decaying surface of the branch. The Fungus, on the other hand, can utilise some of the organic matter that is elaborated by the other members of the firm. One of the puzzles is the way in which a balance is struck and maintained between the two parties. It must be an automatically working pact, and in illustration of the way in which this is elaborated in some forms, we may note how Darbishire has lately traced the regular separation of the fungoid filaments to form a characteristic opening above the Alga-patches, thus furnishing them with what are practically stomata, though not of any familiar build.

One would like to see the clear and pleasant term symbiosis restricted to a usage as precise as possible. It means a mutually beneficial internal partnership between two organisms of different kinds. The fact of "mutual benefit" serves, as well as one can expect, to exclude parasitism, where the advantages, in typical cases at least, are all on one side. The adjective "internal" serves to exclude commensalism, an externally mutually beneficial partnership, such as that between a hermit-crab and the sea-anemones it carries. But what began as symbiosis may sink into parasitism, and what began as parasitism may rise into symbiosis. Thus the fungus that lives in intimate partnership with ling-heather may conceivably

some day become a disintegrative parasite, and it was probably an unimportant mycorhiza before it became a symbion.

Every year adds to our knowledge of symbiotic linkages. According to Miss Raynor and others, though there are dissentients like Knudson, the success of the heather on poor or unready soil is due to its intimate partnership with a fungus whose delicate filaments spread from root to shoot, from leaf to flower, and even into the seed. Many trees have a beneficial fungoid feltwork (mycorhiza) closely associated with their roots. Everyone knows that Leguminous plants, like clovers, lupins, and vetches, have in their gall-like root-tubercles symbiotic bacteria by means of which they

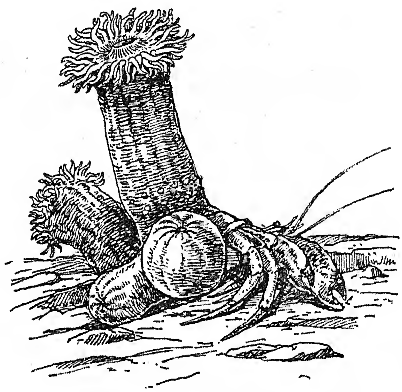


FIG. 36.
Commensalism or Mutually Beneficial External Partnership between a Hermit-crab and Several Sea-Anemones. From a specimen.

are able to fix the free nitrogen of the air. Thus plant joins hands with plant, and nothing succeeds like symbiosis!

Very abundant in the surface waters of the ocean are the microscopic Radiolarians, with shells of extraordinary beauty, fashioned crystal-wise out of flint, or spun of a transparent protein material called acanthin. Now, there are some five thousand different species of these Radiolarians, and as to the numbers of individuals, why, there may be as many in a bucket of water as we can see of stars on a clear night. May it not be that part of the success of these Radiolarians is due to the fact that they all illustrate symbiosis? Inside the clear living matter of these minute and for the most part unicellular animals there are groups of still smaller single-celled Algæ (zooxanthellæ) which are able to effect photosynthesis. The Algæ or yellow cells, as they are called, utilise the carbon dioxide made by the Radiolarian, which in turn benefits by the oxygen liberated by the partner-plants. So if the Radiolarian is not obtaining sufficient extraneous food in the form of minute organisms captured

from the sea, it can fall back on the sugar and the like which its partners have made. In other words, it can absorb products of their photosynthesis, and—why not, if need be?—even digest its partners themselves.

The same may be said in regard to most animals of low degree that are green in colour. For while a few, like the green bell-animalcule (*Vorticella viridis*), have acquired chlorophyll of their own, the great majority are green because of their partners. Thus there are symbiotic Algæ (Zoochlorellæ) in the green freshwater sponges, the green species of freshwater Hydra, some green sea-anemones, many greenish corals, and some green worms.

The symbiosis that has been most adequately studied (by Keeble and Gamble) is that of a small green worm (*Convoluta roscoffensis*), common on the sandy shore at Roscoff, in Brittany. When the tide goes down, the worm comes up; at the first splash of the returning tide the Convoluta retreats again into the sand. This periodicity of movement has become so engrained in the worm's constitution that it persists for about ten days when the creature is transferred to a tideless aquarium. It may even be exhibited in a test-tube! But this is another story; let us keep to symbiosis.

According to Keeble and Gamble the newly hatched Convolutas are colourless, but in the course of a week they establish a symbiosis with the Zoochlorellæ. Unless this is accomplished they seem to die, having apparently lost most of their power of fending for themselves. After the establishment of the partnership there is a period of true symbiosis, and the firm works well. The carbon dioxide formed by the animal is used as food by the plant, which in turn liberates oxygen as long as it is exposed to the light. In the course of time, however, there is a change in the relation, for the Convoluta not only absorbs the carbon compounds that may diffuse out from the Zoochlorellæ, it begins to digest its partners as such. Yet they seem to multiply rapidly enough to meet the demand!

All the cases of probable symbiosis have not been so thoroughly demonstrated as this case of Convoluta, but there is strong reason to believe that many insects, such as cockroaches and larval death-watches, have partner-yeasts in abundance in their food-canal, and that these assist in a very important way in the fermentation or digestion of the food, which is often of a dry-as-dust nature. Some other animals have partner-moulds and many have beneficent bacteria that certainly help in breaking down the food. The bacteria find shelter and fodder, but it is difficult to prove that they are restricted to these intestinal situations. Similarly there is strong evidence that some luminescent animals, notably cuttlefishes, owe their luminosity to colonies of bacteria, allied to the one that illumines haddocks hung up to dry. But here again the proof of a mutually beneficial partnership is very far as yet from being

adequate. Dr. L. R. Cleveland has made a careful study of certain beautiful infusorians that have their exclusive home in the food-canal of many kinds of wood-eating Termites. The infusorians find shelter and fodder, and the Termites or White Ants cannot thrive on their dry food unless their partners (should we call them "symbions", "symbionts", or "symbiotes"?) are present. But symbiosis it is, and we now see that it may be between plant and plant, between plant and animal, and also between animal and animal.

PARASITISM

So far we have discussed the mutually beneficial linkages between two different kinds of organisms, and distinguished external commensalism from internal symbiosis. But parasitism is a one-sided nutritive relation, which is more or less injurious, yet not usually fatal to the host. It is a relation which relieves the parasite from most of the activity or struggle that is usually involved in procuring food; and thus it tends to favour or induce some degree of simplification or degeneracy. The parasitism may be (*a*) between one animal and another, e.g. between tapeworm and dog; or (*b*) between an animal as host and a plant as parasite, e.g. the salmon infested with a Saprolegnia fungus; or (*c*) between one plant and another, e.g. dodder on clover; or (*d*) between a plant as host and an animal as parasite, e.g. the ears of wheat infested by a minute threadworm (*Tylenchus tritici*), which causes "ear-cockles". (*e*) In rare cases, e.g. Bonellia, the male is a parasite of the female.

VARIETY OF PARASITIC RELATIONS.—Parasitism takes many forms and occurs in many degrees, so that hard-and-fast definition is impossible. An organism may be parasitic during one period of life and independent at other times; thus the larval stages of the hookworm live in the soil, the adult stage is reached in man's intestine; or again the young forms of the horsehair worms (Gordius) occur in insects, whence the adults emerge into the water. The parasitism of the strange Copepod Crustacean (*Lernæa branchialis*), dommon on the gills of the haddock, is confined to the female, and does not begin until after pairing has taken place. In two or three of the Angler-fishes of the Lophius tribe, which inhabit the mid-water zone, intermediate between surface waters and abyssal, the male is actually an external parasite of the female.

The parasite may be externally associated with the host, like the mange-mites on dogs; but this ectoparasitism has also its grades, varying with the extent to which the host is punctured or penetrated by the parasite. Thus the very degenerate parasite Crustacean Sacculina protrudes visibly on the ventral surface of the parasitised

crab, but its root-like absorptive outgrowths penetrate through and through its host, and its bean-like adult stage is actually a bulging out like a hernia. The larval stage of Sacculina is a free-swimming nauplius. It is thus not such an easy matter as it seems to distinguish between outside and inside; for when an ectoparasite is sedentarily fixed to the skin and yet absorbs food by an intruded portion of its body, it partakes of the nature of both, and combines their advantages. Yet we hardly think of a sedentary plant-mite as an endoparasite, though it too may permanently insert its head into the victim. Moreover, it becomes, as will be seen, no easy matter to decide whether small animals, such as other mites, that wander about on the surface of an animal's body, are to be regarded as parasites or not. Some are only scavengers; others draw blood; and others deposit eggs in the skin of their host. On the whole, however, there is a general distinction between ectoparasites and endoparasites.

EPIPHYTIC AND EPIZOIC RELATIONS.—Parasitism must be distinguished from epiphytic or epizoic relations. An epiphytic plant grows on another plant without deriving any nourishment from it, as in the case of orchids perched on trees, or of the green Algæ and lichens on bark. Similarly microscopic green Algæ live on the surface of the coarse hairs of the Brazilian tree-sloths, and many a seashore crab carries a garden of seaweeds or an incrustation of barnacles upon its shell. But if the crab, such as *Hyas araneus*, has itself implanted these Algæ, and if there is evidence that the Crustacean is usefully masked, while the plant is benefited by being carried about, then the relation passes into commensalism, i.e. a mutually beneficial external partnership between two organisms of different kinds.

An epizoic animal may live attached to another animal without deriving any nourishment from it, as a bunch of barnacles may be attached to the flattened tail of a sea-snake, or as a Tunicate, a False Oyster (Anomia), a Serpulid worm, a Polyzoon colony, and a Sponge may all be found together on the shell of a Whelk. But if the sponge (e.g. Suberites) should mask a hermit-crab ensconced in the empty shell of a periwinkle, and should be benefited by its association with the vigorously active animal, then the epizoic relation becomes a commensalism. Various marine animals, such as hydroids and even sea-anemones, live attached to large Laminarian seaweeds, but without any nutritive relation, cases which have to be distinguished from animals that habitually browse on the seaweed, like the beautiful "pellucid limpet" (*Helcion pellucidum*). Freshwater sponges are often epiphytic on the stems of aquatic plants in rivers and lakes; and by the sides of the Amazon, when the water is low, they may be seen at a considerable height on trees!

SHELTER-ASSOCIATIONS.—While the contrast between a parasitic relation and an epizoic or epiphytic one is in most cases clear, there may be some difficulty with what are called "shelter associations". Thus the little pea-crab *Pinnotheres pisum* is often found off English coasts sheltering in the mantle cavity of the Norway Cockle; and other members of the Pinnotherid family occur in other bivalve molluscs, as well as in worm-tubes and corals. A small bivalve is commonly embedded in the cellulose tunic of Ascidians. The slender fish called Fierasfer insinuates itself tail-foremost into the end of the food-canal of sea-cucumbers, and it also finds its way into some large bivalves and starfishes. It feeds independently like any other fish, but it seems to enjoy the shelter of animals in which there are active currents of water. When the Holothurian is placed in water with insufficient aeration, the Fierasfer comes out and rises to the surface taking gulps of air. A small fish, Amphiprion, with resplendent colours, lives inside a large sea-anemone, hiding itself deeply when disturbed. It does not seem to do either good or harm to the sea-anemone, but it is said to die when it is dissociated from its "host". This may serve to illustrate how these relations shade into one another.

Similarly some insects find shelter in plants on which they do not feed. A spider may frequent a particular flower; another makes its web below the insect-attracting margin of the pitcher of a pitcher-plant. Many ants live in hollow stems and thorns, but feed elsewhere; so they get nothing but shelter from the plant and confer no benefit. But, in other cases, the sheltering ants feed on secretions exuded by glands on the leaf base, or leaf-tips, of which the inhabited thorn is a stipule. In this case the ant has good reason to guard its leaf from other ants, sometimes leaf-cutters, and promptly nips off the intruder's head accordingly. These ants may thus be viewed as a bodyguard; yet it is prudent to add that some naturalists regard the evidence as unconvincing. Some plant-mites live in little shelters ("domatia") on the plants they frequent, and it is difficult to draw a line between those that puncture the plant and those that simply clean the epidermis. The moist spaces between the leaves of the epiphytic Bromeliads of tropical forests afford shelter to an astonishing number of more or less epiphytic insects; and their inter-rela tions with their habitat are sometimes so subtle that any sharp classification becomes impossible. Yet after all, is it not pushing logic to pedantry, and non-evolutionary besides, to seek to put every grade of inter-relation into a separate pigeon-hole? There are also puzzling epiphytic shelter-associations between plant and plant; one of the best known being the occurrence of the Alga, Nostoc, in certain parts of the water-fern, Azolla, and in certain liverworts, also. The Alga thus finds a sheltered and uniformly moist habitat, but it is not known to do either good or harm to its

bearer. Instances need not be multiplied; it is clear that parasitism, being a one-sided nutritive relation, can be distinguished from shelter-associations. These may indeed develop conversely towards symbiotic partnership, as in the case of the Algæ and fungi which combine into Lichens, in various ways the most successful organic partnership reached in Nature.

PARASITES, COMMENSALS, AND SYMBIONS.—From commensalism, defined as a beneficial *external* partnership between two organisms of different kinds, ectoparasitism is distinguished by being one-sided, being more or less prejudicial to the host. From symbiosis, defined as a mutually beneficial *internal* partnership between two organisms of different kinds, endoparasitism is also distinguished by its one-sidedness. As the definitions here adopted are historically justified and convenient, it seems undesirable to use "symbiosis" loosely for the intimate living together of two kinds of organisms, and then to subdivide it into parasitism and commensalism, as is proposed by Coulter, Barnes, and Cowles in their excellent *Textbook of Botany*, 1911. On this usage a mutually beneficial nutritive partnership, e.g. between clover and its tubercle-forming bacteria, is called "reciprocal parasitism", and "commensalism" is used to include "those cases of symbiosis in which two or more organisms live together with possible benefit to some or all of the symbions, but with injury to none". Without denying the logic of this treatment, we think that it is more naturalistic, more serial and more convenient, to abide by the ordinary usage, i.e. to distinguish endoparasitism from symbiosis, and ectoparasitism from commensalism.

But emphasis must also be laid on the fact that parasitism is a *nutritive* relation. The ecologists just referred to emphasise this, as in distinguishing among plants (*a*) the independent "autophytes", which obtain all their food from inorganic sources, and (*b*) the dependent "heterophytes", "whose existence depends upon antecedent or coexistent organic forms, because they derive at least a part of their food from organic sources". These heterophytes they then divide into saprophytes, which obtain food from dead organic matter, and parasites, which obtain food or food materials from living organisms. In this classification of nutritive habits, a special corner is needed for carnivorous plants, which obtain their food partly from inorganic sources and partly from the animals they capture. Among the bacteria and other plants that live in the alimentary tract of animals, it is sometimes difficult to draw a clear line between those that live on non-living material and those that attack living tissue.

STRICTER ANALYSIS OF PARASITISM.—The biological concept of parasitism is too often blurred by uncritical usage. When

an animal is found to be infested externally or internally by other animals which are habitually present and are not found living independently, and when there is some degree of dependence between the infesting animals and the other, the term parasitism is used without distinctions. But as ecology progresses to clearness beyond the old "natural history" from which it arises, we must more clearly distinguish the various scenes or stages of parasitism. Consider some of these: a flea, promenading over the skin and puncturing here and there for blood; a tick, firmly fixed with its mouth-parts deeply inserted in the dermis; a follicle-mite, such as the common "black-head" often seen on the human face (*Demodex folliculorum*), with its whole worm-like body embedded and absorptive, and only its head showing; a larval red harvest-mite (Trombidium) sometimes felt burrowing in the skin after a gooseberry feast or a grass picnic; the microscopic larva (cercaria-phase) of a Bilharzia in the act of burrowing from the surface of man's skin towards the intestinal or renal blood-vessels; the large maggots of the ox warble-fly, which have come to lie passively under the skin, resting after a prolonged internal journey, and awaiting subsequent pupation in the soil; the full-grown female Guinea-worm, lying in a long coil beneath the skin, and until a sore is formed.

These are but instances of the manifold gradations of habit among parasites which attack the surface of another animal.

Similarly for endoparasites, there is great diversity. Many Infusorians and many Nematodes live in the terminal part of the intestine on the putrefying undigested food-material; they can hardly be called symbions except in special cases, but they do little harm. Tapeworms and the like have their head attached by suckers or hooks or sometimes proboscis to the wall of the intestine; but this has no nutritive significance, for it is the whole long surface of the body that absorbs the digested food of the host. Here is a passive mode of life, almost eluding the struggle for existence, and here also is unmistakable degeneration. Another grade is illustrated by many parasites which depend not on the food of their host, but on the living tissues; and here again a distinction may be drawn between, say, bladder-worms (the cystic phase of tapeworms and other cestodes) growing in a muscle and forms, like Sacculina, which absorb lymph or other fluids from the surrounding tissue, and others, like larval Ichneumon-flies, that directly devour the living tissues of their hosts. The formidable hookworm (Anchylostomum) sucks blood from the intestinal wall; the liver-fluke (Distomum) feeds on the blood of the sheep's liver; but the malaria organisms and many others are in the blood stream itself, destroying the red blood corpuscles. Not a few cases besides Sacculina and its kindred are known where the parasite castrates its host.

PARASITISM AND PREDATION.—The concept of true parasitism would be clearer if there were a separate sub-concept for those cases where the infesting organism lives an energetic predatory life; and is thus not so much a parasite, as a veritable beast of prey devouring its host from within, or, in the case of some ectoparasites, from without. From a broad physiological outlook, parasitism is a negative reaction to the struggle for existence; it implies the discovery and adoption of a mode of life along the line of least resistance. On this view the diagnostic feature of true parasitism is its very evasion of strenuous struggle and individual endeavour. To put it more metaphorically, the swimmer becomes a drifter. Yet the larvæ of an Ichneumon-fly, which are hatched out within a caterpillar and proceed to devour it from within, are hardly less predatory than the lion which devours the antelope from without. These Ichneumon grubs have none of the degenerative stigmata of thoroughgoing parasites. Similarly, while many of the Protozoon parasites, like Gregarines, are sluggish throughout a great part of their life, and may even remain for a long time within the same cell, it is more difficult to apply the strict term parasite to such organisms as the exceedingly active Trypanosomes that cause Sleeping Sickness and allied diseases. They have their quiescent phases, no doubt, but much of their life is spent in charging about among the blood corpuscles at high velocity, though undeniably entering them at last. Many of the Protozoa—especially in the entirely parasitic Gregarines and other Sporozoa—are much simplified cells, but that cannot be said of the Trypanosomes, which are highly specialised flagellate Infusorians, and might well be ranked as unicellular predatory animals that work destruction from within, and this especially in an unwonted host, like man or horse.

And again, as regards ectoparasites, is not the definition somewhat blurred by including such types as the flea? That it is more habitual than a leech in its blood-sucking does not make it less predatory. Its compressed body may be adaptive to escaping capture as it moves swiftly among the hairs of a mammal's skin, but it has no marks of degeneracy in its adult life. It is on an ecological level quite different from that occupied by such types as the mange-mites of the dog. Our point is that the concept of parasitism becomes more useful when habitually predatory types, external or even internal, are placed at its very beginnings, if not positively excluded.

CLASSIFICATION OF PARASITIC ANIMALS.—Protozoon parasites are illustrated (*a*) by the entire class of Sporozoa, including among its half-dozen orders, not only the Gregarines, but types like the Malaria organism (Plasmodium); (*b*) by some Rhizopods, such as the Amœbæ of man's intestine in dysentery, and in his gums in pyorrhea; and (*c*) by some Infusorians, such as the mouthless,

ciliated, multi-nucleate saprophytic Opalina of the frog's rectum, and (perhaps) also the many predatory forms, like the Trypanosomes of sleeping sickness.

There are no parasitic sponges, though many are epiphytic or epizoic. Among Cœlentera there are but a few instances; thus a polyp (*Polypodium hydriforme*) occurs on the ova of the sterlet (*Acipenser ruthenus*). More than one medusoid (*Cunina parasitica*, etc.) are found in close nutritive dependence on other members of their group. The extremely simple and thus perplexing Mesozoa, Dicyema, and its allies, are all parasitic; some of them are possibly extremely degenerate worm-types.

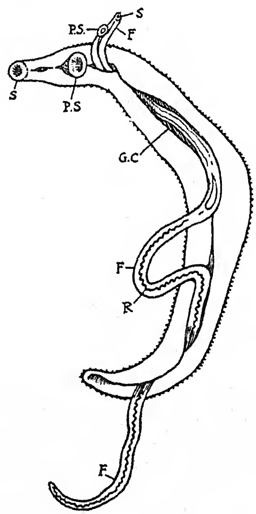


FIG. 37.

Bilharzia or *Schistosomum hæmatobium*. After Looss. The male, about three-fifths of an inch long, carries the longer female (F) in a groove (GC); S, the suctorial mouth; PS, the posterior adhesive sucker; R, part of the reproductive system of the female.

In the phylum or series of flat-worms (Platyhelminthes), a few members of the class Turbellaria are parasitic, one in marine Molluscs, another in or on Holothurians. The members of the allied class of Trematodes are all either ectoparasites or endoparasites. The rare Temnocephalids adhere to freshwater crayfishes, crabs, turtles, etc., but do not feed on their hosts. This Platyhelminth series has its bathos in the Cestodes, which are all endoparasitic, both in their encysted (bladderworm) and adult (tapeworm) stages. All the Nemerteans are free-living, unless two or three found on crustaceans can be called parasites. The aberrant and leech-like Malacobdella

found on a common British bivalve (*Cyprina islandica*) does not seem to do more than capture a share of inswept organisms.

In the phylum or series of round-worms (Nematohelminthes) numerous Nematodes are truly parasitic, while the others are saprophytic; but it is difficult to draw the line, for many of those inhabiting the alimentary canal of higher animals find their whole nourishment in the half-digested food or in the putrefying undigested residue. Many of these *internal saprophytes*, for that is what they should be called, are active and even agile. It is otherwise with the allied and formidable hookworm, which sucks blood from the wall of the food-canal, and also with the gapes-worms, which grip and suck, even to choking, the windpipe of chickens and young pheasants.

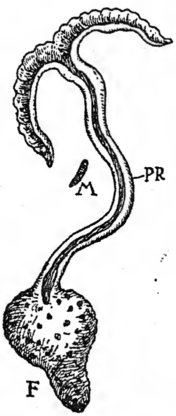


FIG. 38.

Sex Dimorphism in the Green Marine Worm Bonellia. The female (F) has a body about the size of a prune, while the pigmy male (M) is of microscopic dimensions, about 1·5 mm. in length.

Distantly allied to Nematodes are the Echinorhynchus types, thoroughgoing parasites without mouth or food canal. They are digenic, i.e. requiring to pass from one host to another if their life-cycle is to be completed. In this case the passage is from Arthropod to Vertebrate; thus *Echinorhynchus gigas* of the pig passes its larval stage in the grubs of cockchafers and the like; and *E. proteus* of pike, trout, and minnow has its larva in the common freshwater crustacean (*Gammarus pulex*).

Parasitism is very rare among Chætopod worms, but the mouthless pigmy males of Bonellia and its ally Hamingia live—surely as parasites—within the oviduct of the females. Other curious forms (Discodrilida) are found on freshwater crustaceans, Branchiobdella on the gills of the common European crayfish (*Astacus fluviatilis*) and its American ally on the corresponding "crayfish" (Cambarus)

of the Eastern States—a parallelism so close as surely to be of evolutionary suggestiveness, for these two parasites seem to be genuine members of the earthworm order (Oligochæta), though unlike these they are without locomotor bristles, and hold on by suckers and bite with chitinous jawplates. In these two respects, they exhibit a convergence towards leeches, no doubt in adaptation to a similar mode of life. Leeches (Hirudinea) themselves should be regarded as predatory, but incipiently parasitic. Land-leeches often exert themselves to effect attachment to passing animals, as even man sometimes finds to his cost. Certain perplexing forms (Mysostoma)—perhaps offshoots from primitive Annelids—which form galls on Crinoids, are much degraded in relation to their parasitic mode of life. A few Rotifers (e.g. Albertia) are parasitic in or on freshwater worms. Another (Seison) occurs on an interesting primitive marine crustacean (Nebalia); Discopus attaches itself to a holothurian (Synapta); and *Callidina parasitica* to the limbs of some freshwater crustaceans (Gammarus and Asellus). But the reality of the parasitism requires reinvestigation in most cases; the linkage seems sometimes nearer that of commensalism.

While there are no parasitic Echinoderms, the habit is common among the lower Crustaceans, especially among Copepods, many of which are called "fish-lice" (e.g. Caligus and Lernæa). Many grades occur, for the association may be temporary or permanent (after the early free larval stages), and it is often confined to the females. On the other hand, the male may be reduced in size, and even become a parasite on the female, as in Chondracanthus. Allied to the barnacles (Cirripedia) are the peculiar Rhizocephala, e.g. Sacculina already mentioned, which is so often to be noticed by shore-collectors as a bean-like protrusion from the ventral surface of the abdomen of common shore crabs, as well as on our edible species. Its story has been so well made out by that admirable marine zoologist Delage, that it is well worth following in some detail. It starts life as a free-swimming nauplius larva, it develops into a Cyprid stage, and fixes itself to the back of a young crab, and pierces the small circle of uncalcified membrane around the base of one of the few large bristles of this region. It then loses almost all but its head, the thorax and abdominal regions degenerating to form a minute tube through which the head then slides (somewhat as one may do with the tip of an inturned glove finger!) The head thus sinks into the crab, and eventually, as maturity is approached, what remains of the body tube grows outwards, and protrudes on the abdomen. The full-grown sac consists mainly of hermaphrodite reproductive organs, nourished by numerous absorbent root-like processes which spread from the otherwise degenerate head, and penetrate deep into and through the tissues of the crab. Sacculina lives for about three years, arresting the crab's growth, and in the

case of males so altering its host's constitution that its testes degenerate, and are replaced by a small ovarian structure, which may sometimes even produce ova, though whether capable of fertilisation or not, we cannot yet say. In short, the Sacculina effects "parasitic castration". There are various related forms, one of which (Sesarmaxenos) occurs on a freshwater crab in the Andamans. As Darwin first showed in his classic Monograph, some of the true barnacles, normally hermaphrodite, have small parasitic, "complementary" males: others are unisexual, yet the males are also minute and parasitic on the females. Even among the higher crustaceans, parasitic forms occasionally occur, notable in certain Isopods which infest other members of the class. The young forms are free-living and male, the adults are parasitic and female; but it seems that while all females pass through a male stage, without genital ducts, those males that become functional never grow up into females. Many of these Epicarids cause parasitic castration of their hosts. Some of them afford good instances of hyper-parasitism, i.e., of parasite upon parasite. Thus a very common Mediterranean species (*Danalia curvata*) is parasitic on a Sacculina (*S. neglecta*), which in turn is parasitic on a spider-crab (Inachus). Somewhat similar Isopods infest the gill-chambers, mouth-cavity, and skin of various fishes. In many of the species, if not in all, the young free-swimming forms function as males, but afterwards settle down and become females—an interesting convergence of physiological changes in two very distinct families.

Parasitism is not to be expected among the winged insects, but many wingless types, such as lice, are true ectoparasites; and some free-living winged insects, like warble-flies (Œstrus, etc.) have parasitic larvæ. The blood-sucking lice (Pediculidæ) constitute an order, which Latreille called Parasita, ectoparasitic on mammals. They are marked by absence of wings, small head, with simple eyes or none, and large abdomen, and by the adaptation of the claws to clutch the hairs; yet it cannot be said that lice are particularly degenerate, since still not very far removed from the predatory. This is even more marked in the case of the biting lice or bird-lice (Mallophaga), which occur on birds and a few mammals, feeding not on blood, but on skin cells and fragments of feathers and hairs. Some birds shelter numerous Mallophaga, thus the hen has nine; but occasionally a particular species of bird-louse is restricted to a particular species of bird. Related species are often found on related hosts. This specificity is often to be noted in parasites, yet there are others, such as the liver-fluke, that have many different hosts. But as to the Mallophaga, there does not seem to be much of the parasite about them; they are skin-scavengers, and the same may be said of fleas and of the sheep-tick (*Melophagus ovinus*), a wingless Dipteron. It is different, however, with the larvæ of bot-flies and warble-flies,

which illustrate temporary parasitism. A curiously isolated case of alleged parasitism is a little beetle found exclusively on beavers. In many of the Ichneumon-flies and related types, which lay eggs in caterpillars and the like, the predatory larvæ are themselves parasitised. This "hyper-parasitism" is sometimes carried far. Thus a certain caterpillar (*Hemerocampa leucostigma*) which defoliates many trees in the north-eastern United States has 23 primary parasites (17 Hymenoptera and 6 Diptera); these have 13 secondary parasites (all Hymenoptera); and these again 2 (perhaps 5) tertiary parasites; indeed, one of these (Asecodes) may be in some cases not tertiary, but quaternary!

Among Arachnids various degrees of parasitism are illustrated by mites and ticks, some externally adherent, others burrowing in the skin, a few, like the bee-mite, penetrating deeply. Sometimes placed in the vicinity of Arachnids are the vermiform Pentastomids, (e.g. Linguatula), found in the nasal cavities and frontal sinuses of carnivores, crocodiles, snakes and some other flesh-eating animals. Apart from a few Gasteropods, such as *Entoconcha mirabilis* attached to blood-vessels in Synapta, there are no parasitic molluscs. Nor are there any parasitic Vertebrates except the pigmy males of some Angler-fishes; and the predatory Myxinoids, like the Hag-fish (much lower than a true fish), are sometimes reckoned as temporary endoparasites of certain fishes.

A survey of parasitic animals shows the widespread distribution of this mode of life. But it is of rare occurrence (*a*) among types that are sensitive to lack of ample aëration; thus there are no parasitic Echinoderms; (*b*) among types that breathe dry air; thus, endoparasitism is relatively uncommon among insects; and (*c*) among types whose shape of body is markedly unsuitable, such as the long-legged spiders.

PARASITIC PLANTS.—More briefly let us discuss parasitism in the Vegetable Kingdom. Plants may be parasitic in or on animals, a striking case being the rod-like fructification of a fungus (Cordyceps) that grows out to a length of several inches from the head end of a parasitised insect-larva, such as a caterpillar or a grub. The common house-fly is often seen dying from the ravages of a fungus, *Empusa muscæ*, the spores forming a white powder around the moribund insect; another species is from man's point of view very useful as a check on the multiplication of green-flies. It is but rarely, however, that wild animals in natural conditions fall victim to fungoid or even bacterial attacks.

An estimate of the number of parasitic animals that infest plants varies according to the strictness of the definition of parasitism. The gall-mites (Phytoptids), which cause swellings on many plants, have only two pairs of legs, very simple mouth-parts, and a worm-

like body, thus showing some marks of the degeneration so often associated with thoroughgoing parasitism; but it seems hardly justifiable to rank the numerous leaf-miners and stem-borers as parasitic in the strict sense. They have adopted an internal predatory mode of life. Similarly it seems doubtful if a species of Trypanosome that lives in Euphorbias is really a parasite. It is obvious, yet worth noting, that a plant, from its very nature, is capable of surviving internal and external injuries which would be very serious if the host or victim were an animal.

Of plants parasitic on plants there are multitudinous instances with great diversity, though not approaching that illustrated by animals parasitic on animals. At the one pole are parasitic moulds, mildews, and rusts, etc.; at the other pole the dodder on the clover or the toothwort on the roots of the hazel.

Very clear among parasitic plants is the contrast between partial and complete parasitism. Thus the mistletoe is a partial parasite, for it is usually believed to take nothing but water and salts from the tree on which it grows. Its own green leaves are capable of normal photosynthesis. Yet there is no hint of reciprocity on its part, as has been experimentally corroborated by defoliating the bearer. In contrast to the mistletoe, the leafless and chlorophyll-less dodder (Cuscuta) is a familiar illustration of complete parasitism, for it depends on its host not only for water and salts, but for its organic food as well, in the form of carbohydrates and proteins. The common and pretty Eyebright and Yellow Rattle (Euphrasia and Rhinanthus) are good instances of partial parasites; for while they have green leaves and absorb soil-water, they get on better if their roots come into organic continuity with the roots of neighbouring plants, such as grasses. The related cow-wheat (Melampyrum), though green, cannot survive without external aid. In the Alpine Tozzia, belonging to the same family, the whole of the first year is spent as a complete parasite underground; but in the second year there rises a flowering shoot with yellow-green leaves. In the broom-rape (Orobanche) the parasitic dependence has gone still further, for the seeds will not germinate unless they are in contact with a suitable host, such as the broom; there is no chlorophyll, and apart from the underground absorbing roots and stock, there is only a flower-stalk with a few scales. The extreme simplification of the vegetative system is seen in the Rafflesias, where "the whole vegetative body of the parasite may live inside the host plant, reduced to a spreading weft of undifferentiated filaments—root, stem, and leaf alike lost". From this degenerate vegetative body, none the less effectively adapted for absorption, there burst forth strange and gaudy blossoms. One of them, *Rafflesia Arnoldii* of Sumatra, is the largest of known flowers, with the immense diameter of a yard.

The vegetative body of Rafflesia may be reasonably called degenerate, but it must be asked, following MacGregor Skene, whether all the simplifications of parasitic plants deserve this term, and whether the simplifications are to be regarded as *primarily* associated with the parasitism. The beginnings of reduction, e.g. in leaves and in amount of chlorophyll, are often to be seen quite apart from parasitism. Some reduction in assimilatory power, or some other inferiority in competing with rivals in crowded conditions, may prompt root-parasitism or some other parasitic dependence. And when the habit of parasitism or partial parasitism has begun, it is not unreasonable to suppose that degenerative variations, e.g. towards "golden leaves" or towards albinism, would be more likely to survive because of the abundant nourishment supplied by the host.

ORIGIN OF PARASITISM.—(*a*) Many animal parasites, such as some of the Nematodes, may have begun as saprophytes. Several flies that normally lay their eggs in putrefying animals may similarly utilise the abrased skin of one that is still living. (*b*) Many animals are cryptozoic, given to hiding themselves, or negatively heliotropic, inclined to seek out narrow and shaded passages; and this is another way in which parasitism may arise. The commonplace is often overlooked that the host is not to the parasite another organism, for that would mean an incredibly subtle awareness of the situation, but merely a convenient and attractive environment. (*c*) It is likely that parasitism often arose when the struggle for existence was extremely keen, when even slightly open doors were welcome. As already indicated, the most characteristic feature in parasitism is probably some weakness or passivity of constitution, a "disposition" more inclined to drift than swim. Just as some such animals became cave-dwellers, others became parasitic. (*d*) Crustacean parasites are particularly interesting because they afford many illustrations of parasitism restricted to the females; in whom, in addition to the passivity frequently associated with the sex, the parasitic habit might arise in connection with the advantage of securing sheltered nooks for liberating eggs or offspring. (*e*) Where sex dimorphism in growth—increased in the female and diminished in the male—becomes very pronounced, as in Bonellia, many Copepods, also, and even two mid-water Angler-fish, there would be an advantage to the survival of the tiny males, and even to the females themselves, in this degeneration of males, since securing fertilisation, and so maintaining the species. In the Anglers alluded to, which occur sparsely in thinly peopled waters, the female carries the minute male; and all his nourishment is derived from an organic connection between his head and the blood-vessels of some part of her skin. In the extreme sex dimorphism of many Rotifers,

the problem has been solved in another way, namely by a relapse into parthenogenesis. (*f*) It is also possible that parasitism has in some cases evolved from shelter-associations and from commensalism. Indeed, it is here often difficult to draw the line. (*g*) It is likely that parasitism has often arisen from another form of parasitism! That is to say, the parasite of a freshwater crustacean may become adapted to become secondarily parasitic in a freshwater fish which habitually feeds on the first host. An elaboration of this extension of range comes about when different phases of life are restricted to each of the two hosts, a common punctuation being that an asexual phase occurs in the one host and a sexual phase in the other. Leuckart, who discussed this problem very carefully, in connection with tapeworms, came to the conclusion that the "intermediate host", (e.g. mouse), which now contains the young non-reproductive phase, was the original host, and that the "secondary or definitive host" (e.g. cat) has been found later. Yet it is conceivable that in some cases the intermediate hosts of the immature stages have been intercalated. When there are two hosts, there is usually, though not invariably, this relation between them, that the definitive host eats the intermediate host as part of its normal diet. Thus the cat's tapeworm has its bladderworm stage in the mouse; but it is not by eating water-snails that the sheep is infected with liver-fluke. A sometimes serious parasite of man (Echinococcus), too common in Iceland and Northern countries, was found by a parasitologist to be derived from the dog as intermediate host. Thus in most cases it can be eliminated by insistence on kennels outside the house, and better scrubbing and sweeping out of dust from within. Perhaps more than Icelanders would profit by knowing these facts and applying them.

DAMAGE DONE TO HOST.—It is usual to emphasise the fact that it is not in the parasite's interest to destroy its host; but this is verging on the anthropomorphic. Parasites cannot be credited with a policy. In many cases, e.g. follicle mites in man, or Monocystis in earthworms, the parasite is small compared with its host, and the damage done may be unimportant. Yet a heavy infection with threadworms may be fatal to a horse; and if ichneumon-grubs are regarded as parasites (an interpretation above criticised) they are obviously fatal to their caterpillar hosts. Much often depends on the numerical strength of the infection; thus a few gall-larvæ, each imprisoned in its gall, may be regarded as trivial, but the multiple infection of a black-currant bush with "big bud" mites may soon be fatal. Then a distinction must be drawn between parasites that multiply in their host, as Nematode worms often do, and those, like tapeworms, that cannot increase in numbers within the same animal. It may be that rapidly destructive parasites have been

persistently eliminated in the course of evolution, as would naturally happen if they destroyed their host before becoming themselves reproductive. But the large fact to be emphasised is that in many cases a give-and-take relation is established between the parasite and the host, such that the parasite does not get the upper hand and the host is not too seriously prejudiced. In the intestinal caeca of the grouse there are often thousands of almost invisibly transparent Nematodes (*Trichostrongylus pergracilis*), whose early stages are found on the heather. If the grouse is otherwise in good condition, its Nematodes seem to be unimportant, but if the grouse be constitutionally below par, the parasites may multiply excessively (10,000 in one bird) and fatally. When parasites or quasi-parasites prove quickly destructive, it is usually when they find their way into a new host that offers great advantage, as by having no natural counteractives to their influence and increase. This is familiarly illustrated by microbes when they find themselves in a new host, which thus may not have powers or time to develop the wonted natural checks, such as "anti-bodies".

As to the nature of the damage done by parasites, it may be enough to mention the most outstanding: (*a*) robbing their host of much half-digested food (ninety specimens of a big and long tapeworm (Bothriocephalus) in one patient!); (*b*) absorbing much blood (as in the case of hookworms in man, and of gapes-worms in chickens); (*c*) causing serious pressure on adjacent parts, e.g. the sturdie-worm (*Cœnurus cerebralis*) on the sheep's brain; (*d*) perforating the intestinal wall (as large threadworms sometimes do); (*e*) blocking passages, as bee-mites (*Acarapis woodi*) in the thoracic tracheæ of hive-bees with "Isle-of-Wight" disease. More unusual is castration, e.g. that of crabs infected by parasitic Epicarids; or the formation of open sores by emerging guinea-worms; or the production of a cancerous growth in fishes by the irritation of a Nematode worm (Gongylonema).

It has been proved that some animal parasites are toxic. (*a*) Thus the malaria organisms produce toxic substances in the red blood corpuscles, and these are liberated when the corpuscles break up. Sarcosporidia of sheep contain toxic substances which are fatal in very small quantities when injected into rabbits. (*b*) When the big cysts of *Tænia echinococcus* burst, and the fluid escapes into the body cavities, there is violent poisoning; and the fluids of other bladderworms have been shown to be toxic. (*c*) Some adult tapeworms (e.g. *Dibothriocephalus latus*) are also toxic, producing a hæmolytic lipoid substance, which is liberated when segments disintegrate, and perhaps also as a secretion. Thus the anæmia of human patients becomes more intelligible; and it is probable that other tapeworms liberate toxic substances. (*d*) Ascaris produces in the routine of its metabolism volatile aldehydes and fatty acids,

like valerianic and butyric. If the worms die and disintegrate in the intestine, the liberation of these substances may readily produce toxic effects; and students have often suffered cutaneously after dissecting the large Ascaris of the horse. The poisoning observed in the formidable disease of trichinosis, due to man's eating infected ham, either raw or insufficiently cooked, is probably due to products of the parasite's metabolism as well as to disintegration of the surrounding muscle in the case of the pig host.

Of great interest medically is the fact that the irritation produced by the pressure of the parasite may lead to cancer-like growths in the host. Thus cancer-like results are produced in man's bladder by the Egyptian Bilharzia worm, and sarcoma of the rat's liver is believed to be instigated by the bladderworm stage of *Tænia crassicollis*, which occurs as a tapeworm in the food-canal of the cat. But the most striking case is that worked out by Professor Johannes Fibiger of Copenhagen, to whom was awarded one of the 1926 Nobel prizes. He investigated in detail a threadworm or Nematode, *Gongylonema neoplasticum*, which lives in cockroaches. If the infected insects are eaten by rats, the Nematodes pass into their stomachs and by their irritation instigate the growth of malignant tumours.

It must be noted, however, that, in an enormous number of cases, the presence of parasites is neither here nor there. A *modus vivendi* is often established between parasite and host, and no appreciable harm results. But, if the host be otherwise debilitated, the parasites may multiply fatally. The introduction of a parasite into a new host is, of course, in many cases fatal, as when Trypanosomes are introduced by tsetse-flies into man or horses, or into any other appropriate host that is without natural defences against the intruders. It is not known that the Trypanosomes found in the blood of tropical African antelopes do their hosts any appreciable harm.

ADAPTIVE CHARACTERS OF ANIMAL PARASITES.—The assumption of a parasitic mode of life is a habitudinal reaction to the intensity of the struggle for existence; and while there is no discharge from that war, intimate dependence on another organism for food and shelter implies to some extent a life of ease. What adaptations are there to the parasitic mode of life?

(1) Many parasites have structures that lessen their risk of dislodgment, e.g. the adhesive suckers on the head of tapeworms, the gripping hooks of the hookworm, the attaching hold-fasts of parasitic Copepods.

(2) Many parasites are specially adapted for the absorption of food from the host. A very simple adaptation is the great increase of absorptive surface in tapeworms, which may be many feet long.

In Sacculina the absorptive outgrowths ramify like roots right through the body of the parasitised crab. The head of the pigmy parasitic male of the mid-water Angler has grown continuous with the tissue of the female who carries him. A strange Gasteropod parasite (Entoconcha) has its head thrust into a blood-vessel of its holothurian host. When the available food from the host is very abundant, it may be utilised by the parasite in a somewhat uneconomical fashion; thus some Nematodes ferment glycogen into valerianic acid, carbon dioxide, and hydrogen, which is far from making the most of the material. In tapeworms the whole surface of the body absorbs liquid food. Parasites deeply imbedded in tissues must be nourished by the lymph, just as if they were parts of the host.

(3) It is characteristic of many thoroughgoing endoparasites that they can survive in conditions where free oxygen is apparently very scarce. In most cases they seem to obtain a sufficient supply from the blood or tissues of their host, just as if they were parts of the body. There is no modern corroboration of the older view that some multicellular parasites can live anaërobically.

(4) Many parasites, such as Nematodes, Crustaceans, Insects, and Mites, have a chitinous cuticle, which is very resistant, e.g. to bacteria and to digestive juices. But the presence of a thin-skinned tapeworm in man's intestine or of delicate Infusorians in the horse's stomach requires some explanation, and there is some evidence that their insusceptibility to the digestive juices is due to their development of an "anti-body".

(5) There are some noteworthy adaptations in connection with reproduction. Thus resistant egg-shells are characteristic of Platyhelminths, and the tapeworm's liberation of an entire joint, capable of some independent movement, must often be advantageous. The difficulty of securing fertilisation, when the parasites do not occur in large numbers together, is met in various ways, e.g. (*a*) by a very prolonged association of the sexes, as in Bilharzia, where the male carries the female, or in Chondracanthus, where the female carries the male; (*b*) by self-fertilisation or autogamy, as in the liver-fluke; or (*c*) by an emergence of the sexually mature forms into freedom, as in Horsehair-worms (Gordiacea). There are some very remarkable cases, notably the Trematode, *Diplozoon paradoxum*, where two mature hermaphrodite individuals are united in permanent cross-fertilisation. In the genus Wedlia, two individuals are found together inside a cyst, a smaller one—the male—imbedded into a protrusion of the vesicular posterior body of a larger one, the female. But each individual shows traces of the gonads of the opposite sex, so that this looks like a secondary abandonment of hermaphroditism, when arrangements for securing fertilisation had been in the course of time established. Quite another circumvention of the difficulties is a relapse into parthenogenesis, as in some

Nematodes, such as a common intestinal parasite of man in Tropical Asia (*Strongyloides stercoralis*).

(6) Deserving consideration by itself is the prolific multiplication. Leuckart's estimates have been often quoted, that *Tænia solium* may produce 42 million eggs in a year, and an Ascaris 64 millions. It is possible, no doubt, to discover some free-living animals still more prolific, such as a starfish (*Luidia ciliaris*), which Mortensen credits with containing 200 million eggs, but there are not many instances of such extraordinary fecundity; not even among fishes. Moreover, it is possible to compare the huge number of eggs produced by many a Trematode, the liver-fluke's being estimated at 50,000, with the small number produced by a not very distantly related free-living Turbellarian of the same size.

The eggs and larvæ of parasites are often subject to severe elimination; the chances of death are enormous. Therefore, in the course of the evolution of parasites, variants in the direction of increased productivity would have survival value. Thus the race now continues with a large margin. It may also be granted for some cases that the conditions of the individual life, e.g. rich and abundant food, will favour prolific reproduction.

SOME EVOLUTION PROBLEMS.—(1) It must not be facilely supposed that the adaptive peculiarities of parasites illustrate individual modifications that have hereditarily accumulated until they have become racial characters. Organisms that have begun the parasitic mode of life because of certain constitutional weaknesses may continue to show congruent germinal variations, some of which may have selective value. (2) It must not be too confidently assumed that all the diagnostic peculiarities of parasites are as such engrained hereditary characters. Many of them may be individual structural reactions to the peculiar conditions of life, which recur with each generation. An organism's characters develop as the outcome of environmental, nutritional, and functional nurture operating upon hereditary nature. There is much to be said for the view that the pigmy male of Bonellia suffers arrest of development partly because it absorbs the secretion on the proboscis of the female. More attention should be paid to phenomena like those of "physogastry" in the guests of the white ants, where extraordinary deformations of body come about in probably direct individual reaction to the unwholesome conditions of life. Experimental inquiry is also needed to show whether some of the specific characters of nearly related parasites may not be modificational. To test this experimentally, nearly related species in different hosts should be exchanged in early life. (3) It may be noted that many parasites probably illustrate the results of "isolation", which narrows the range of inter-crossing. For not only is the host in some ways like an island, to take the

simplest form of "isolation", but the combination of circumstances which secure fertilisation, diffusion, a second host, and so forth, is often so subtle that it operates as an isolating evolution-factor.

BIOSOCIAL COMPARISONS.—It is an old story that the very word *parasite* was taken over by zoologists from its classic usage, in application to self-invited and pertinacious guests at the rich man's table; and the inverse comparison has again become increasingly frequent in modern times, thus frankly inspiring the well-known *Parasitism, Organic and Social,* by Massart and Vandervelde, the latter since eminent as a political leader in Belgium, and to this day helpful at Geneva. And many years ago, long before that book, it was no small surprise to one of us when writing the article "Parasitism (Animal)" in the *Encyclopædia Britannica* (9th edition), and when also comparatively fresh from a sound training in classical political economy, to note the amazingly close similarity, often wellnigh to identity, between these two distinct and separately developed presentments of fully attained material success in life.

ILLUSTRATIONS OF PLANT ECOLOGY

The Ecology of Plants, as we have already explained, is the study of their relations to their environment, and to one another, and to animals. It is a physiological inquiry, but it deals with plants in the plural, in their associations and linkages, not with the life of the individual plant. It is in the main the old-fashioned "Natural History of Plants"; and it is far more of a "field science" than plant morphology or individual physiology. The ascent of sap is a problem in the physiology of the individual, though it has its ecological aspect, in reference to the seasons, and to particular surroundings; but the inter-relations between flowers and their insect visitors are typical problems in ecology.

HISTORICAL NOTE.—The word ecology is due to Haeckel, who used it to denote the study of organisms in their relations with their animate and non-animate environment. As a synonym the term "Bionomics" was suggested by Ray Lankester; but Ecology is preferable in its suggestion of studying the living creature in its home or *oikos*. Very unfortunately the general term "Biologie" is used in exactly the same sense by many German naturalists. While the study of plants in relation to their habitats, enemies, pollinators, seed-scatterers, parasites, and so on, has a long history behind it, it is only within the last fifty years that plant ecology has been taken very seriously. The study of the linkages between flowering plants and their insect visitors received a great impetus from Darwin, who

had his precursor in Christian Konrad Sprengel, and Darwin's interest in his *Insectivorous Plants* and *Climbing Plants* was also characteristically ecological; but it is only within recent years that there has been a precise study of plant-associations, such as the characteristic vegetation of moorland, mountain, swamp, and desert, and a determined attempt to interpret structural and functional peculiarities as adaptive to the surroundings in the widest sense. Kerner's well-known *Natural History of Plants* may be noted as the first large treatise on Botany to place the ecological aspects in the forefront.

SURVEY.—An attempt must be made to map out Plant Ecology; and that is not easy because of the manifoldness of the relations involved. In his erudite *Biologie der Pflanzen,* Neger proposes the following arrangement: Adaptations to warmth, to light, to water-absorption, to water as a habitat, to the substratum or soil (edaphic), to increase of mechanical stability, to other organisms, and to the preservation of the species. But this is too elaborate, though less so than most of those that have been suggested. We must be content here with a much simpler outline of the chief problems.

(1) Ways of dealing with the environment (both animate and physical) so as to secure food-materials—including air, water, salts—and so as to facilitate the utilisation of radiant energies, light and heat in particular.
(2) Ways of securing survival against environing difficulties and limitations, including changes of weather and climate and competition with other organisms, including parasites.
(3) Ways of securing the continuance of the race, including, for instance, pollination and seed-scattering.
(4) Ways of securing the intimate assistance of other organisms, notably in symbiosis, epiphytism, and climbing.

While sustenance, for instance, is largely a physiological problem, it becomes ecological when we study the plant's adjustments and adaptations to particular environmental conditions.

The four keywords in this simple grouping are SUSTENANCE, STRUGGLE, REPRODUCTION, and PARTNERSHIPS. Many of the inter-relations between plants and animals have been already referred to in the zoological portion of this ecological section.

SUSTENANCE.—It is convenient to begin with the plant's relation to the soil, from which it absorbs water and dissolved salts. Typically this is effected by means of the roots, and especially by the ephemeral root-hairs which grow out from the cells of the younger parts of the rootlets, just behind the growing tips.

In seaweeds the entire surface of the plant is absorptive, and there

are no true roots comparable to those of higher forms. What look like roots are anchoring structures (rhizoids), and this must be regarded as the primary function, absorption being secondary. Similarly, lichens are firmly fixed to the rocks and the like, sometimes on the mountain-tops, by means of hold-fast "rhizoids", very like root-hairs in appearance, though there are no true absorbent roots. They are also to be seen in liverworts, mosses, and the prothallia of ferns—delicate, threadlike outgrowths of surface-cells, more for attachment than for absorption. In ferns there is a first appearance of true roots like those of seed-plants; and the line of evolution has been the addition of an absorptive to an anchoring function.

Among the many adaptations of roots to particular conditions, the following may be noted. Plants frequenting dunes, where the wind often shifts the sand, may show roots of great length, often extending for yards, and sometimes branching into a network. From these, at intervals, shoots rise above the surface. Good examples are the sand-binding grasses (*Elymus arenaria* and *Ammophila arenaria*) and the sand-binding sedge (*Carex arenaria*), which secure their own survival by gripping the shifting sand over a wide area, and are also of great importance to man in preventing sandstorms, which are apt to smother arable land.

On many tropical shores the substratum is loose and swampy, and more or less flooded by high tides and storms. This difficulty is met in species of Pandanus (so-called screw-palms) by numerous stilt-like roots, which are given off from the stem at various levels and sink down into the loose sand and mud like so many anchors, some descending vertically and others obliquely or in an arch. This circumvention of a difficulty reaches perfection in the Mangroves (mostly species of Rhizophora), where the stilt-roots are very numerous and often very long, forming extraordinary root-thickets. Those trees that go farthest out are most abundantly productive of these adventitious roots, and they form a sort of breakwater to those nearer the firm shore. Schimper notes in regard to a common species of mangrove, *Rhizophora mucronata*, that the stilt-roots are not developed when the tree is cultivated on dry ground. That is to say, the power of forming these adventitious growths is a specific character, but it requires an appropriate nurtural stimulus if it is to be expressed.

The cases of dune-plants and mangroves must serve to illustrate the adaptation of roots to meet peculiar conditions of the substratum, but there are many others. Thus many fig-trees in humid equatorial forests (such as *Ficus elastica*, common in our greenhouses) have extensive superficial roots which spread round the base of the stem like narrow vertical planks, and resist the strain on the tree, which is often, though not always, slender and high.

INADEQUATE FOOD-MATERIALS.—Soils differ greatly in chemical

composition; and there is sometimes a deficiency in salts, such as compounds of nitrogen, phosphorus, potassium, and calcium. But different kinds of plants differ not a little in their requirements, and thus one of the consequences of deficiency in the soil may be that certain species are excluded, while others are favoured. Thus bog-mosses (Sphagnum) flourish best where there is little lime; and there are interesting cases, as in *Gentiana excisa* and *G. acaulis*, of what looks like the splitting of a species into those that cannot stand much lime and those that can.

Just as members of the same species may become large or may remain minute according to the soil (and other environmental factors), this being a matter of individual modification, so there are giant and dwarf varieties of presumed germinal origin which are adapted to luxuriant and niggardly conditions. Thus in the Barren Grounds or Tundra of the Far North, where the soil is often extremely poor, and where other conditions, such as the long winter, are adverse, there are many constitutional dwarfs, such as birch-trees and willow-trees only a few inches in height. Another adaptive characteristic of plants frequenting poor or unready soil is the lengthening of the roots, rootlets, and root-hairs. Neger notes that plants so adapted to make the most of soil that is deficient in certain constituents, nitrogen-compounds in particular, are readily killed if transplanted into a rich garden. The sundew is said to be killed if supplied with "hard" water.

In bog-mosses, which are also very sensitive to more than a minimal quantity of salts, there is a large capillary system between and in the leaves, so that, as everyone knows, they are like sponges in the quantity of water that they can retain. Moreover, the colloidal character of the cell-walls facilitates absorption. The nitrogenous food-materials are chiefly obtained from the rain and the included dust-particles. The same seems to be true of the leaves of the rootless epiphytic Tillandsias, sometimes called "vegetable horsehair", which are abundant on the branches of trees in South American tropical forests. The upper surface of the leaf is in some species thickly covered with peculiar flattened scales or hairs, which absorb the rain-water or the dew and its dissolved particles. There are absorptive hairs on some of the Orchids of the Far East which live high above the ground, and there are Javanese mosses which hang from the leaves of forest trees and absorb water by their whole leaf-surface. In another section we shall refer to cases where scarcity of food-material in the soil is circumvented by partnership with a fungus, as in some heaths, or with symbiotic bacteria, which fix the atmospheric nitrogen, as in all Leguminous plants.

INSECTIVOROUS PLANTS.—The majority of insectivorous (or more strictly carnivorous) plants occur on moorland soil, which is

poor in nutritive salts, or in water-pools in similar places. Thus sundews (Drosera), butterworts (Pinguicula), Venus's Flytrap (Dionæa), and the Sarracenia and Cephalotus pitcher-plants are characteristic of wet moors and swampy places; and most of the Bladderworts (Utricularia) live in moorland pools. Some of the bladderworts are terrestrial, others epiphytic; and most of the pitcher-plants of the Nepenthes type live perched on trees in swampy places. Over four hundred species of Flowering Plants are known to be insectivorous; but 250 of these are Utricularias, 100 are sundews, and 40 belong to the genus Nepenthes, so that the remarkable fact is not that so many plants have taken to this peculiar mode of nutrition, but that there are relatively so few. In a corner by themselves may be placed a few carnivorous fungi, such as *Arthrobotys*

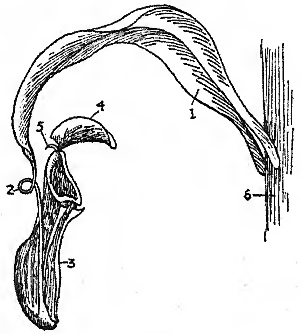


FIG. 39.

A Typical Pitcher-plant, a species of Nepenthes. 1, Stalk of transformed leaf; 2, twist on tendril-like portion; 3, the pitcher itself; 4, the lid; 5, a spur; 6, the stem.

oligospora, living in dung, which catches, kills, and absorbs small threadworms in the nooses of its mycelium, and *Zoophagus insidians*, which does the same for Rotifers.

BUTTERWORT.—We begin our survey of these interesting plants with the least striking, the Butterwort, Pinguicula, of which about thirty species are known from marshy grounds, especially among the hills, in the Old World and the New. They belong to the same order as the Bladderworts (Lentibulariaceæ). A number of plump, glistening yellowish-green leaves form a flat rosette on the ground, and from the centre a slender upright stalk rises for two or three inches and bears a beautiful flower, somewhat like a violet in shape and colour. The leaves have a slightly fungus-like smell, possibly attractive to insects, and they are covered with hundreds of minute stalked and sessile glands, which secrete two digestive ferments, one like pepsin and the other like rennet. Linnæus mentions that the Lapps use the leaves for curdling milk. The secretion entangles small

insects, chokes their breathing tubes, and then serves for digestion. The margins of the leaves are sensitive to touch and turn slightly inwards, thus assisting capture. Particles of sand may provoke a slight inturning, but this is soon reversed. The effective inrolling of the margin follows the entanglement of small insects, which points to the need for a chemical as well as a mechanical stimulus. Like Pinguicula in its mode of insect-capture is the Australian Byblis.

SUNDEWS.—Widely distributed on moors all over the world, except in the Arctic regions and the islands of the Pacific, are the sundews (Drosera), of which about a hundred species are known. On tufts of bog-moss or the like one sees little rosettes of red leaves glistening with drops of secretion, which have earned for the plant such names as *sundew, Sonnentau, Rossolis*. From the centre of the prostrate rosette there rises a short upright stalk, bearing inconspicuous whitish flowers in summer, or more conspicuous seed-pods in autumn. In the common *Drosera rotundifolia* a narrow leaf-stalk expands into a more or less circular blade, the edges and surfaces of which are beset with scores of peculiar somewhat club-like glandular hairs or "tentacles", long and recurved at the margin, very short towards the centre of the blade. On an average there are about two hundred, and the longer ones close down, one after the other, on a struggling insect which has stimulated them. Thus the leaf becomes in an hour like a closed fist. The glandular head of the hair exudes digestive juice and a little formic acid, the latter probably serving to prevent premature putrefaction. For about a week the leaf remains closed, and the absorption of the products of digestion goes on. When this is complete, the tentacles begin to move outwards again, the surplus secretion is absorbed, and the leaf reassumes its original condition—with the chitinous debris of the insects remaining on its surface as tell-tale evidences of its prolonged meal.

The highly evolved hairs are derivable from the glandular hairs familiar on many plants, such as the London Pride and the Catchfly; and its hould be recalled that digestive ferments are common in many plants—in situations so diverse as the flowers of the Yellow Bedstraw and Artichoke, the stem of Clematis, the seeds of the vetch and the latex of the Papaw Tree (*Carica papaya*), the leaves of which are sometimes wrapped round flesh to make it tender. But the tentacles of the sundew have evolved far beyond these beginnings. They are very sensitive to stimulus, they are mobile, and they are absorptive as well as digestive. Up the centre of the hair-stalk there runs a bundle of wood-vessels, which supply the gland with water; and outside these there is a layer of elongated cells lined by a thin film of colourless circulating protoplasm, and filled with a purplish fluid. When the gland of the hair is stimulated with a minute

droplet of phosphate of ammonia, a remarkable change may be watched under the microscope, passing from one coloured cell to another down the stalk ("cytoplasmic aggregation").

The tentacles are more or less indifferent to falling drops of rain; but, as Darwin showed, they are extraordinarily sensitive to solid particles and to certain chemical stimuli. A morsel of human hair, weighing only $\frac{1}{78740}$ of a grain, and this largely supported by the viscid secretion, suffices to induce movement. This seems almost hypersensitive; but it is doubtless important that the plant should react to the light touches of minute midges and the like. Darwin's experiments in connection with chemical stimulus are very interesting. He treated sixty-one leaves of Drosera with droplets of non-nitrogenous solutions, such as sugar and olive oil, and in not a single case was a tentacle inflected. But when sixty-four other leaves were tried with various nitrogenous fluids, such as milk, albumen, mucus, beef-extract, sixty-three showed marked inflection of the tentacles. And when he took twenty-three of the leaves that had served for the first experiment, and treated them with nitrogenous particles or fluids, the tentacles of all save a few were distinctly inflected. Thus a slight trace of nitrogenous substance on the surface of the insects that light on the leaves will serve to induce a movement of the tentacles. Darwin showed that there was peculiar sensitiveness to salts of ammonia, especially phosphate, nitrate, and carbonate, even in infinitesimal quantities. Thus the immersion of a leaf in a solution of phosphate of ammonia, so weak that each gland could only absorb $\frac{1}{20000000}$ of a grain, was sufficient to produce complete inflection of the tentacles.

In some cases the tentacles respond to the contact of inorganic particles, which is obviously unprofitable; but it is interesting to notice that the reaction does not follow unless the contact is repeated twice or thrice, which is what occurs when an insect touches the leaf with its chitin-covered limbs.

Darwin noticed that the tentacles of the sundew moved inwards when the temperature was suddenly increased; and this may perhaps make for efficiency on sunny days when insects are most in evidence. This sensitiveness to warmth has been confirmed, with the interesting detail that it is paralysed when the plant is supplied with water rich in lime-salts, which are absent from the ordinary moorland habitat. Neger calls attention to this as an instance of the delicacy of the physiological poise in some organisms. The nutritional change in this case is but a small one, but it brings about a very striking alteration of habit.

The leaves of the sundew seem to have some attraction for insects, but whether this is due to their colour, their glistening secretion, or their odour, or to all three, remains uncertain. The exudation of the viscid secretion may be slight at first, and involve only one or

two of the outer tentacles, but it becomes more copious, and the stimulus passes to adjacent parts. There is no doubt as to the transmission of the stimulus; and in some species, e.g. *Drosera longifolia*, several leaves may be involved in the capture. But how this is brought about is unknown; it may be that a large insect stimulates several leaves in its struggle.

The experiment has been made of stroking the head of one of the central tentacles with a finely pointed match, the result being that in a few minutes the marginal tentacles begin to move inwards. When the head of a single marginal tentacle is strongly stimulated, it bends in to the short central tentacles, and only then do its neighbours at the margin follow suit. It looks as if the stimulus is conducted outwards, but not inwards, in the leaf-blade. This is curiously like a reflex action in an animal, but there are no nerves or muscles in the plant—only irritable and mobile protoplasm. Yet another resemblance between the sundew and an animal is that quite different stimuli may evoke exactly the same response. Just as a muscle may contract under mechanical, nervous, or electrical stimulus, so the sundew's tentacle may move when touched by a solid body (which produces rapid differential compression, in neighbouring areas of the cell-substance) or by certain nitrogenous substances in solution.

As to the movement which occurs at the base of the tentacle, it is sometimes ranked as analogous to those of growth. This view deserves to be stated. "The basal part is able to renew its youth and start growing again when excited. The growth is unequal and is mainly or wholly confined to the outer or lower side. An increase in length of that side, relative to the upper side, means that the tentacle bends inwards. The straightening or bending outwards takes place by the opposite process of a relative increase in the length of the upper side." (Macgregor Skene, *Common Plants*, 1921, p. 54.) It follows, one would think, that the movements of a full-grown tentacle must be very infrequent, else it would become too long! Moreover, the movements referable to differential growth-rates are much *slower* than in the sundew. Another view is that the movement is due to varying flaccidity in the tissues at the base of the tentacle. For if the turgidity of the inner cells at the base of the tentacle is relaxed by the excitation due to the stimulus, there is no need to invoke *growth* in the outer cells. This is, of course, an intricate question, in regard to which we may profitably agree to differ for a while. After elaborate study Bose concludes that a nervous-like communication from the point of stimulus alters the turgidity of the cells of a motor organ.

The question remains as to the advantage of the insectivorous habit to the sundew. As its leaves contain chlorophyll, partly disguised by the red cell-sap, the sundew can make carbon-com-

pounds for its own sustenance; but the difficulty is in regard to nitrogen supplies, of which the moorland water has little. Thus the sundew is "nitrogen-hungry", and hence the advantage of catching insects whose tissues contain nitrogenous carbon compounds such as proteins. As a matter of fact, the sundew can survive and even seed without any insects, but Darwin's experiments, fully corroborated since, showed that plants fed with insects, fragments of flesh, or particles of yolk of egg, flourished much better than those which were left to themselves but shielded from insects. In some cases the fed plants attained twice the weight of the controls, and produced five times as many flowers and five times the weight of seeds.

Allied to Drosera is the less highly evolved *Drosophyllum lusitanicum*, common in dry, sandy, or rocky places in Portugal and Morocco, and sometimes used by the peasants as a substitute for flypaper. It has a better root-system than its marsh-loving allies, and its long narrow strap-like leaves rise to a height of eight or ten inches. They are interesting in being rolled up in the bud after the fashion of ferns, but backwards instead of forwards. They bear two kinds of glandular hairs, stalked and unstalked. The former exude a viscid gluey secretion which entangles insects, and besides this a little formic acid. But they are not able to move like those of the sundew. The unstalked glands secrete a digestive ferment, and the stimulus comes from the capturing tentacles and also from the formic acid which these secrete. Both kinds of glands share in the absorption. The effectiveness of Drosophyllum may be inferred from the fact that on one occasion the botanist Goebel counted on a plant a year old, which had lived in a greenhouse with open doors, no fewer than 233 distinctly visible flies, entangled on the surface of nineteen leaves. Belonging to the same order, Droseraceæ, is the South African Roridula, in which the "insectivorous habit" is not more than incipient. It may be regarded as a hint of a beginning.

VENUS'S FLYTRAP.—This native of the Carolinas was first described (1768), in a letter to Linnæus, by John Ellis, a London merchant, who was one of the early students of corals. Linnæus called it *miraculum Naturæ*, and we cannot wonder. Like its allies, the sundews, the Flytrap (*Dionæa muscipula*) lives in marshy places. Its brightly coloured leaves form a prostrate rosette, from the centre of which a stalk with numerous flowers rises to a height of 4–6 inches. Each leaf is a trap, consisting of a winged stalk and a bilobed blade, the halves of which are movable on one another. Round the margin of the blade are 12–20 long stiff processes, somewhat suggestive of a trap's teeth; and those of one side interlock with those on the other when the blade closes. Rising from the middle of each half-blade there are three bristles, hinged at their base, and they are especially sensitive to the sideways touch of an insect's feet. When the hairs are thus stimulated the halves of the

blade rapidly close, the movement being due to a sudden collapse of cells along the midrib. But a slower closure may also be provoked by stroking or pressing the surface of the leaf with a splinter of wood, or by a nitrogenous chemical stimulus on the same surface. In ordinary cases the stimulus is due to the insect's feet touching the side of a sensitive hair; and it is interestingly adaptive that a drop of rain falling vertically on a sensitive hair has no effect. According to Macfarlane, mechanical stimulus of Dionæa requires two touches, unless the touch be very powerful; and the touches must be separated by an interval of more than a third of a second. If less than that interval be allowed, no contraction follows, and a third stimulus is then necessary. A neat adaptation is the joint near the base of the hair, where there is a slight constriction, and above that a narrow zone of joint-cells which elongate at one side and shorten at the other, thus enabling the hair to fold down. If it were not for this flexible base, the six hairs would be crushed when the trap closed.

If an insect is caught, there follows a copious secretion of digestive ferment (plus a little formic acid) from glandular cells, which form the attractive rosy patches on the surface of the leaf-blade. This chemical stimulus induces a stronger closure of the trap, so that the insect is squeezed against both leaf-blades. Here again there is adaptation, for the introduction of a non-digestible body does not evoke the secretion, and in the absence of the chemical stimulus there is no second contraction. In normal circumstances a leaf opens quickly if it has closed on a non-digestible body, but if an insect has been captured the trap remains shut for a week or so, during which the booty is digested and absorbed. If the insect that is captured be too large, the trap never reopens; and even in natural conditions a leaf is not able for more than two or three meals in the course of its life. Although the movement of the Flytrap is very different from that of muscle, Burdon Sanderson showed that there is a similar electrical change in both cases; and it is possible that the electrical change is also correlated with the secretion, for so it is in the case of many animal glands. Here again Bose's later work should be referred to.

Experiments with this "carnivorous vegetable", as Bartram called it in 1790, have shown that if it is cheated into closing by inappropriate mechanical stimulus, it soon opens again; and that a repeated cheating induces a state of insusceptibility, during which it fails to respond to a touch which would normally evoke movement. But this does not last long; the "vegetable memory" is short; and after a rest the Dionæa may be cheated again.

Allied to Dionæa is a rootless water flytrap, *Aldrovandia vesiculosa*, which lives in well-sunned pools in south and central Europe and also in Australia and India. There are whorls of 8–9 little leaves, somewhat like miniatures of the Dionæa traps. The two halves of

the minute leaf-blade meet at an angle of about 60°, but after a certain age they are all practically closed. Each half-blade shows (1) marginal bristles, (2) a glandular zone with quadrifid hairs which probably secrete attractive mucus, (3) a non-glandular zone, and (4) an innermost zone with digestive glands and hinged sensitive bristles. These seem to require repeated touches, such as a restless water-flea might well give, before they evoke the full reaction. Within the closed traplet a gas-bubble is formed and absorption of the digested fluid goes on slowly.

Bladderworts.—In marshy lochs and mountain-tarns in Britain there is a widespread occurrence of the Common Bladderwort (*Utricularia vulgaris*), conspicuous for a month or two in summer, when from the floating stem there rises for several inches a slender flower-stalk with somewhat orchid-like golden blossoms, which appear but once in several years. At other times the bladderwort is anything but conspicuous, for it floats in the water and its leaves are small. Like some other thoroughly aquatic plants, e.g. Salvinia, it is rootless, a peculiarity which may be correlated with the absorptive power of the whole submerged surface, rather than with the carnivorous habit.

The bladderwort belongs to the order Lentibulariaceæ, which also includes the butterwort, and there are about 250 species representing the genus in all parts of the world. But many of these are terrestrial, and a number are epiphytic.

With the single exception of the epiphytic *Utricularia neottioides*, the bladderworts have many leaflets transformed into pinhead-like "bladders" or traps. Each is a hollow chamber, about $\frac{1}{10}$ inch in longest diameter, entered by a transparent valve which opens inwards only, and allows of no egress, for it shuts instantly, as if with a spring, against a thickened collar around the mouth. Six or seven stiff hairs project from the opening into the water, and secrete an attractive mucus mixed with a little sugar. It may be mentioned that the superficial secretion of mucus is common in submerged water-plants.

It has been shown experimentally that the secretion of the hairs is attractive to small crustaceans, popularly known as water-fleas, some belonging to the order of Copepods, while others, e.g. the very common Cypris, are Ostracods. This difference in diet corresponds to differences in the habitat of the species; thus *U. vulgaris*, which floats near the surface, is a Copepod-catcher, whereas *U. intermedia*, which is submerged near the substratum, is an Ostracod-catcher. In some cases there is a capture of other small animals, but the restless exploratory movements of the water-fleas make them very likely booty. It is probable that they touch the yielding door of the eel-trap-like bladder by chance; in any case, there is no doubt that they enter and are imprisoned. The slime probably abets suffocation,

for it has been observed that death follows quickly in young and abundantly secreting bladders, which are coloured reddish with anthocyan in the common species, while the prisoners may swim about for days in those that are older, and have their anthocyan changed into blue. Over the internal surface of the bladder there are minute quadrifid hairs, and it has been experimentally proved that these absorb organic substances. After the bladders have been fed with a little of the fatty substance called lecithin, globules are seen in the quadrifid hairs. There is also a secretion of a digestive ferment, and along with that a little benzoic acid, which probably prevents premature putrefaction of the victims. The peculiar four-armed hairs are connected by intergrades to the much larger external hairs; and it should be noticed that similar hairs occur on various aquatic plants, e.g. *Callitriche verna*, which have no carnivorous habits. Finally, the evidence is completed by Büsgen's observation that bladderworts from which all water-fleas were carefully excluded did not thrive so well as those in quite normal conditions. As a possible instance of a play within a play, we may mention, though with some doubt, the observation that the water-spider (Argyroneta) sometimes rifles the little bladders of Utricularia.

In the summer months the straggling stem of the common bladderwort, with its much divided slender leaves and its hundreds of "bladders", floats at the surface, and grows at one end as it dies away at the other. Towards the end of summer the life of the plant becomes concentrated in the thick-set terminal tuft, which is weighted with reserve products. As in some other aquatic plants, this terminal tuft breaks off and sinks to the bottom, remaining in a resting state through the winter. In spring it begins again to grow, and somewhat lightened rises to the surface to recommence the cycle. This fact led A. P. de Candolle and some other botanists to the mistaken view that the bladders functioned as floats. In 1852 de Candolle said that the young bladders were filled with mucus, which, being heavier than water, kept them at the bottom, but the mucus was gradually replaced by gas, which buoyed the plant to the surface. There is no doubt as to the sinking of the terminal tuft and its floating up again, but the bladders are not concerned. As Darwin showed, a bladderwort floats as usual after its bladder are all cut off—which must have taxed even Darwin's patience. Moreover, there are many non-aquatic Utricularias which have nevertheless thousands of bladders. There is no doubt whatever that the bladders serve as traps, even in the terrestrial species. They are known to capture minute terrestrial animals which creep about in damp places or on the mossy stems of trees.

It is ecologically interesting to notice special adaptations to the diverse habitats of bladderworts. The aquatic forms have sometimes air reservoirs which act as buoys for the upright flower-stalk;

the epiphytes have often water-reservoirs which enable them to survive the dry season; the terrestrial species, though rootless like all the others, have little processes or rhizoids which descend into the ground, especially at the base of the flower-stalk, and serve to steady the latter as well as to absorb water.

Allied to Utricularia is the rarer Genlisea, found in marshy places in Brazil, Cuba, and Angola. It is rootless except in the seedling, and the upright stem is beset with two kinds of leaves. The ordinary foliage-leaves are spatulate, and the others, far fewer, are strange traps. Each is tipped with two spirally twisted glandular arms, which secrete mucus, and are intricately equipped with hairs and processes which allow of the entrance of very small animals and make exit next to impossible. Then follows a long neck, also lined internally with downward directed hairs, and near the base there is a little bladder-like expansion. These strangely transformed leaves grow into the swampy ground, and serve to anchor the rootless plant, and also to entrap minute animals. Goebel points out that the Butterwort is near the starting-point of a series, with Genlisea diverging in one direction and the various Utricularias in another.

PERCHED PLANTS OR EPIPHYTES.—In North Temperate countries the most familiar epiphytes are certain lichens, which often spread profusely on the branches of trees. But there are also a few unicellular Algæ, of the Pleurococcus type, which make the stems green, especially in damp weather. Higher on the scale are the tree-mosses, and here and there one sees a polypody fern perched far above one's head. In the cleft of a tree, where there has been an accumulation of dust and humus, and occasionally a dead bird or the like, there is the beginning of soil, and such plants as Herb Robert (*Geranium robertianum*) and species of Willow-herb (Epilobium) may be seen in flower. But these flowering plants are only casual epiphytes.

Constant epiphytes are characteristic of humid tropical forests, and many of them belong to the Orchids, Aroids, and Bromelias. They obtain their necessary water from rain trickling down the branches, or directly from the water vapour of the air; and the mineral salts are obtained from dust particles and sometimes from a slight accumulation of organic debris. Very characteristic is the widely distributed "Vegetable Horsehair" or "Spaniards' Beard" (*Tillandsia usneoides*), which hangs down in long silvery-grey streamers from the high branches. In this species there are neither leaves nor roots, the whole plant being reduced to the numerous long thread-like stems. While many epiphytes, like the one just mentioned, are perched on tree-tops, they occur at all levels to a few feet above the ground. This of itself is enough to suggest that the

advantage is getting out of the crowd rather than getting nearer the light.

Among the common adaptations of epiphytes may be mentioned: (*a*) structures for absorbing water, e.g. by a spongy tissue covering the aërial roots; (*b*) structures effecting attachment, e.g. non-absorbing anchoring roots; (*c*) reduction of transpiration, e.g. by developing of a firm cuticle or by having little or no foliage; and (*d*) the specialisation of seeds for attachment.

It occasionally happens that a plant perches on an animal, and this association might be called epizoic, were it not that this term is used (like epidemic) in connection with the spreading of some animal diseases. On littoral animals, such as limpets and mussels, there is sometimes a growth of seaweeds, already referred to in connection with "masking", and a lobster is occasionally found with a thick draping. When the animal is a rapid mover there may be some advantage to the Alga by promoting aëration. Strangest of all linkages of this sort is the occurrence of minute Algæ on the rough hairs of the South American Tree-Sloths.

CLIMBING PLANTS.—Darwin's strong ecological interest, so marked in connection with Insectivorous Plants, was also illustrated in regard to climbers; see his *Movements and Habits of Climbing Plants* (1875). As the habit has developed among many different orders of plants and in all parts of the world, there must be some general advantage, which may be described in a general way as escape from crowded struggle and from extreme shade by getting on to the shoulders of other plants. To this it should be added, from our point of view, that the climbing plant is often marked by a relative weakness of stem which prevents it standing upright, and by the elongation of internodes which facilitates leverage. To others it seems to involve fewer assumptions to suppose that a climbing plant is one which has adapted itself to climbing by using its resources to form large vessels and by effecting quick growth at the expense of lignification.

We shall follow Darwin's convenient grouping of climbing plants into five grades: scramblers, root-climbers, twiners, leaf-climbers, and tendril-bearers, though there are, as usual, gradations between these.

SCRAMBLERS.—The brambles on an old-fashioned hedge or by the side of a copse may serve as a starting-point. With vigorously growing stems, sometimes many yards long, they ramp among the adjacent stronger plants, and they are helped by their spines. There is no special adaptation; the brambles lever themselves on the shoulders of their neighbours. Yet the New Zealand *Rubus squarrosus* is able to climb more vertically, just like Ramblers among roses. The Climbing Palms or Rotangs (e.g. *Calamus extensus*) have

barbed branches which help them to insinuate themselves. Very familiar, too, is Jack-Run-the-Hedge (*Galium aparine*), entirely unable to support itself, yet helped up by the backward-turned hooks on its stem and leaves. In the end it is often highest of all the plants in the hedge, sometimes crowning the successful bramble. Another common hedgerow plant is the Bittersweet (*Solanum dulcamara*), a near relative of the nightshade and the potato, which is on the whole a "leaner" on its neighbours, but illustrates the gradations that everywhere occur by being also to some extent a twiner.

ROOT-CLIMBERS.—Conveniently by themselves are the root-climbers, like the English Ivy, in which the stem gives off adventitious roots binding the plant to its support. In the Ivy these attaching roots, usually turning brown in colour, have entirely lost the normal absorbing function. They are negatively heliotropic—that is to say, they grow out on the shaded side of the stem. In experimental conditions of very dim light they emerge all round. Among the other root-climbers may be mentioned the common *Tecoma radicans* of the Southern States, the Vanilla orchid, the often-cultivated Climbing Fig, various Arums and Bignonias. It should be noted that some have absorptive as well as attaching rootlets, and that attaching rootlets may occur on climbers that also use other methods, as in some Virginia Creepers.

TWINERS.—A higher grade is that of the twiners, well illustrated by hop and honeysuckle, and by many of the lianas of the tropical forest. The growing tip of the main stem is constitutionally compelled to grow against the pull of gravity, and it exhibits "a bending and bowing movement" or "revolving nutation", usually to the left, or opposite to the hands of a watch, as in dodder and bindweed, but sometimes following the sun, as in hop and honeysuckle. As Darwin said, the youngest part of the growing hop shoot "may be seen to bend to one side and to travel slowly round towards all points of the compass, moving, like the hands of a watch, with the sun". Some twiners, such as the Chili Nettle (Loasa) and the Bittersweet, move indifferently in either direction. Darwin found that the average period for a complete revolution in the hop on a summer day is 2 hours 8 minutes; but the rate varies greatly for different plants. It is slower at night. If a growing twiner is inverted, it reverses the direction of its movement; and it will not twine unless gravity is acting on it in the erect position, and unless an almost vertical support is at hand.

If the growing part strike on a suitable support, it is arrested by the contact; but as the free portion continues growing and nutating, the same occurs higher up; and so the twining goes on. As some of them attain to a great height, as is sometimes illustrated by the honeysuckle, it is not surprising to find a special development of sap-conducting tissue.

To the twiners and scramblers of the tropical forest the general name liana is often applied, and they form a prominent ecological feature. Macgregor Skene writes: "In the great forests of the tropics the trees find competitors and often conquerors in the mighty creepers—the lianas—which twine their tough, slender stems round supporting trees and round each other, crushing the life out of the less resistant by constricting the conducting tissues, as does the ivy with us. Hanging in festoons, climbing in inconceivable confusion, they render the forest impassable to all but determined axemen. And they reach out beyond the supporting trees, carrying their leaves to the light above the roof of the forest, held up by pillars of dead stems which they themselves have strangled." Of this "woodland warfare" in which the lianas play such deadly part there is an extraordinarily vivid picture in R. L. Stevenson's *Woodman*.

LEAF-CLIMBERS.—In Clematis and Tropæolum the stalk of the leaf is sensitive to contact and bends round a support; in Gloriosa it is the tip that effects attachment. These types are approaching tendril-bearers, but there is no marked specialisation of the climbing structure. In the young leaves of the Climbing Fumitory (*Corydalis claviculata*) the whole surface of the young leaf is sensitive to contact, and bends towards the side on which pressure is exerted. Thus the support is clasped.

The sensitiveness of the leaf-stalks is sometimes exquisite; thus Darwin observed one which responded to the slight but continued pressure of a loop of soft thread, weighing only $\frac{1}{16}$ of a grain. The region below the contact tends to become stronger, with more woody tissue, approximating sometimes to a stem. It is interesting to notice that in some species of Clematis and Tropæolum the petioles show little mobility or sensitiveness, but whether they have lost these qualities or never had them, who can tell?

TENDRIL-BEARERS.—A tendril is a specialised climbing structure, very sensitive and mobile, and the tendril-bearers, such as vines and passion-flowers, represent the highest grade of climbing plants. Although it is a morphological, not an ecological question, we may notice here the variety of structures that may be transformed into tendrils. A tendril may develop from an entire leaf (e.g. in one of the vetches, *Lathyrus aphaca*), from a leaflet (e.g. in the Sweet Pea), from a stipule (e.g. in Smilax), from a shoot (e.g. in Bryony), from an inflorescence (e.g. in Vine and Passion-flower), and even from an aërial root (e.g. in Vanilla). This illustrates one of the methods of Organic Evolution—the making of a new structure out of something much older.

The sensitiveness of tendrils to contact surpasses that of animals. Thus Darwin notes in regard to the tendrils of the common pea: "Whilst young and about an inch in length, with the leaflets on the

petiole only partially expanded, they are highly sensitive; a single light touch with a twig on the inferior or concave surface near the tip caused them to bend quickly, as did occasionally a loop of thread weighing $\frac{1}{7}$ of a grain." He gave the highest place to the tendrils of the passion-flower: "A bit of platinum wire $\frac{1}{50}$ of a grain in weight, gently placed on the concave point, caused a tendril to become hooked, as did a loop of soft, thin cotton thread $\frac{1}{32}$ of a grain." The tendril's response to touch followed in 25–30 seconds in the passion-flower.

Like the tips of growing shoots in general, the tendrils move slowly round (nutating) in circles or ellipses. In the common pea the tendril takes about an hour and a half to complete its elliptical orbit. In the much thicker and more sluggish tendril of the vine the ellipse is so narrow that it looks as if the movement was from side to side.

In the course of its nutation the tendril may touch some adjacent support, round which it proceeds to curve. This curvature movement is due to *differential growth*. The touched side, which is in most tendril-bearers the lower, immediately begins to grow more slowly, the opposite side grows more rapidly; the result must be curvature. But as the free tip of the tendril goes on growing and nutating, a new point comes into contact with the support, and another curvature follows. This goes on till the whole of the free part has been attached.

Then the behaviour of the tendril changes. The coiled part becomes more woody and grips the support firmly. Then, perhaps after a day or two, the straight portion, between the attachment and the base of the tendril, twists into a tight spiral, reversed once or twice, and afterwards becomes woody. The advantage of the corkscrew is twofold; it draws the shoot nearer the support, and it forms a cable that does not readily snap in the wind as an uncoiled part would be apt to do. This is admirably illustrated by Darwin's observations on the bryony. "I have more than once gone on purpose during a gale to watch a Bryony growing in an exposed hedge, with its tendrils attached to the surrounding bushes; and as the thick and thin branches were tossed to and fro by the wind, the tendrils, had they not been excessively elastic, would instantly have been torn off and the plant thrown prostrate. But as it was, the Bryony safely rode out the gale, like a ship with two anchors down, and with a long range of cable ahead to serve as a spring as she surges to the storm."

An interesting point is that the spiral twisting of the lower part of the tendril does not occur when there has been a merely temporary curvature, such as is seen when the tip of the tendril has been affected by casual pressure. This is what might be called a negative adaptation.

As a climax of positive adaptation we may notice the adhesive

discs borne by tendril-branches in some Virginia Creepers. In the Japan ivy (*Psedera tricuspidata*) the tendril-branches end in little knobs, which not only broaden out into discs when contact is effected, but secrete a mucilage which makes fixation doubly sure.

If a tendril fails to find any suitable support it dies, and similarly the adhesive discs of Virginia Creeper (*Ampelopsis veitchii*) harden. But Neger cites Czapek's description of a remarkable plasticity in *Entada polystachya*, a strong liana of Tropical America. The leaves bear branched tendrils, which twist and harden in the ordinary way if contact with a support is effected. But if no support is reached the tendrils develop leaflets, which help in photosynthesis.

The chief advantage of the climbing habit is that it enables the climber to spread out its leaves in the open light, and yet secures this with an economy of supporting tissue. The rattan palm (Calamus) may be over seven hundred feet in length, but its stem is relatively slender. On the other hand, the disadvantage of the habit is that the liana may smother or strangle or overweight its supporting tree, with the result that both are brought fatally to the ground.

In addition to marked mobility and sensitiveness, exaggerations of qualities seen in some measure in all the higher plants, the climbers show (1) flexibility and firmness in the axis (often associated with a peculiar splitting up of the wood into numerous separate strands, and a reduction of pith); (2) a lightness of build, so that there is not overstrain on the actually attaching structures, such as tendrils and hooks; (3) a proportionately high development of the sap-conducting system, seen especially in an enlargement of the calibre of the wood-vessels when the climber has reached a certain height and thickness and has begun to lose much water from its expanded foliage.

As to the origin of the climbing habit, which occurs in so many different orders and is effected in so many different ways, it is reasonable to regard it as a specialisation of the nutation and sensitiveness seen in most plants that have an axis and appendages. The recent emergence of a twining variety of one of the snapdragons (*Antirrhinum majus*) is suggestive of the possibilities that may lie latent and unsuspected. It arose as a mutation, we cannot tell how; and in addition to its incipient twining habit, it shows compacting of wood and reduction of pith. Yet there is no recognisable advantage in the new habit in this particular case, for the stem is strong enough to stand on its own legs. The mutation breeds true, and shows that a climbing race might arise as a germinal variation.

Evolution.—Some light on the evolution of climbers in the wide sense is afforded by experiments on the elongation of stems. Shade and moisture tend to evoke prolonged growth of stems, as is sometimes familiarly illustrated by potatoes sprouting in a damp and almost dark cellar, or by strawberry runners spreading under

the cover of the dense foliage of adjacent plants. The palmetto in dry open places has practically no above ground stem, "while in moist woods, plants of equal age have long slender trunks several metres in height". So is it with many other plants in dark or in moist places,

We suggest then, that the shaded and humid conditions of the forest may act as stimuli on individual plants generation after generation, and that the peculiarities, especially the more superficial, are *in part* modificational, i.e. are impressed on each successive generation. But this is only part of the answer, for there must, we think, be added the suggestion that the shaded and moist environment has favoured those plants with an intrinsic tendency to grow long shoots and to exaggerate mobility and sensitiveness. Every summer one may see in a deeply shaded wood the elimination of unsuitable types whose seeds have been sown by birds or the wind.

One step farther may be ventured. It may be suggested that the environmental conditions of shade and humidity act as variation-liberating stimuli, and that they tend to evoke in the germ-cells particular kinds of variations, such as those that find expression in a twining habit.

As for the detailed structures that assist in climbing, the tendrils in particular, it is hardly possible at present to get beyond the general Darwinian view that variations are of frequent occurrence and that special climbing organs have been derived from stems, branches, flower-stalks, leaves, leaflets, petioles, midribs, and even roots. The widespread occurrence of these adaptations is striking, for, as Darwin pointed out, more than half of the fifty-nine alliances into which Lindley divided flowering plants include climbers of some kind or other.

It is fitting that we should close this section by quoting the last paragraph of Darwin's *Climbing Plants*. "It has often been vaguely asserted that plants are distinguished from animals by not having the power of movement. It should rather be said that plants acquire and display this power only when it is of some advantage to them; this being of comparatively rare occurrence, as they are affixed to the ground, and food is brought to them by the air and rain. We see how high in the scale of organisation a plant may rise when we look at one of the most perfect tendril-bearers. It first places the tendrils ready for action, as a polypus places its tentacula. If the tendril be displaced, it is acted on by the force of gravity and rights itself. It is acted on by the light, and bends towards or from it, or disregards it, whichever may be most advantageous. During several days the tendrils or internodes, or both, spontaneously revolve with a steady motion. The tendril strikes some object, and quickly curls round and firmly grasps it. In the course of some hours it contracts into a spire, dragging up the stem, and forming an excellent spring. All move-

ments now cease. By growth the tissue soon becomes wonderfully strong and durable. The tendril has done its work, and has done it in an admirable manner."

MYCORHIZA.—As a striking example of mutually beneficial living together, we take Mycorhiza (i.e. fungus-root), where a partnership has been established between a fungus and the root of some plant, usually green. The association occurs in two grades of intimacy. In some cases, as in the beech, the fungus forms an external network around the roots; in other cases, as in orchids, the fungus penetrates into the interior. In a few plants, as in Vanilla, the fungus is *both* outside and inside.

The external root-fungi (ectotrophic) may form a feltwork so dense that the roots of the plant do not come into contact with the soil; but there are many gradations. Sometimes, as in beech, the fungus is a soil mould, allied to Penicillium; sometimes the threads are very like those that form the mycelium of truffles and mushrooms. The difficulty of identification is due to the fact that the partner fungus does not normally form reproductive organs, which are more characteristic features of a fungus than its vegetative system. Yet recent skilful culture has elicited reproductive developments, thus showing that Boletus, common in larch-woods, supplies their mycorhiza; and the like for other well-known fungi, common in forests.

The internal fungoid (partners endotrophic) seem to be more specialised types, not ordinary soil fungi; they send their threads into certain cells of the root, where they often form coils around the nuclei. Special suctorial structures are often developed. When predominantly external root-fungi send hyphæ into the tissue of the root, they usually spread between the cells, not into them.

An external association between fungoid hyphæ and roots is so very common, often occurring in more than half the species of a random collection of flowering plants, that it seems useful to try to restrict the term mycorhiza to cases where the feltwork is pronounced and constant, or where it is associated with some peculiarity of root growth, or where the seedlings do not flourish in sterilised soil. But even when these conditions are insisted on, the number of external root-fungi is very large. What used to be regarded as a peculiarity of forest-trees, such as beech and pine, is now known to be an exceedingly common linkage.

Very interesting experiments on internal mycorhiza in Orchids were made by the French botanist, Noël Bernard, too early lost to science. He found that the well-known difficulty or impossibility of growing imported orchids from seed was due to the fact that germination does not take place, or does not succeed, except in the presence of certain fungi, which must sometimes be of a particular species

for each kind of Orchid. These fungi are normally abundant in the tropical soil; and as the orchid seeds are very small, very numerous, and wind-borne, there is little risk of their not finding suitable fungi in the orchid's native haunts. But it is far otherwise when a new orchid is brought to a new hothouse in Europe.

If the seeds of an orchid be sown on a sterilised medium, which ordinary seeds would utilise, there may be slight swelling, but there may be no germination or no more than a beginning. If the appropriate fungus is supplied, it penetrates into the cells of the orchid embryo, and all proceeds normally, except that the development is in most cases very slow. When inappropriate fungus hyphæ are supplied, they may induce germination, but in most cases this soon comes to a standstill. This may be because the fungus is too strong for the orchid embryo and parasitises it, or because the orchid embryo is too strong for the fungus and digests it. It should be noticed that the seeds of some kinds of orchid can be stimulated and partnered by one out of several species of fungus; but Bernard convinced himself that the most highly evolved orchids were the most fastidious, so to speak, in regard to their partners; and it is generally agreed that the converse proposition is true, that the most generalised fungi can enter into partnership with several different kinds of lower orchid.

Recent experiments by Professor Knudson of Cornell University indicate that the indispensability of the orchid partner-fungi has been exaggerated. Certain orchids can flourish and flower without partners; and a little sugar in the culture in which the minute seeds are sown may serve to induce germination and the growth of vigorous seedlings.

We cannot go into the details of a fascinating story, but it is important to notice some of the grades of the partnership. Thus the seeds of the Lady's Slipper Orchis (Cypripedium) will not germinate at all without fungus contact; in Cattleya, very common in greenhouses, germination occurs without the presence of the fungus, but the seedling is very short-lived; in Bletia the seedling can live independently for some months, but after that, in the absence of its natural partners, it stops growing.

As to the physiological nature of the symbiosis, only tentative statements can be made. First, as regards germination, it may be that the fungus supplies a ferment which stimulates; but it must also be noted that the seeds of orchids are poorly equipped with reserves, and the fungus may be of service in establishing a very early nutritive connection with the soil. It is interesting to recall the fact that the spores of the "Stag's Horn Moss" (Lycopodium) do not develop beyond the 5-cell stages in cultures that are devoid of fungi.

But what of the mature plant? It is probable that some of the

external or chiefly external root-fungi serve to absorb water and salts from the soil, and thus function as extraneous root-hairs. It is noteworthy that many of the plants that have external root-fungi are poorly equipped with root-hairs. As to the investing fungus, it cannot be benefited unless it also sends hyphæ into the root; but when it does so there may be a profitable absorption of carbon-compounds which the green plant has made.

When the mycorhiza is strictly internal and intracellular, the puzzle of interpreting the symbiosis is even greater. How is the green plant benefited when the fungus has little or no connection with the soil? And although the host often digests the fungoid hyphæ, this may be comparable to phagocytosis in animals, when active amœboid cells digest intruding micro-organisms. In the case of the mycorhiza, the digestion may be the host's method of keeping the fungus within bounds. One would not, indeed, press the point that what organic material the flowering plant may absorb from the endotrophic fungus has been previously absorbed by the fungus from the cells of the flowering plant. For it may well be that the organic matter is *changed by the fungus* into more useful form, just as happens in the symbiotic organisms of some insects, e.g. cockroaches and wood-boring beetle larvæ, which can alter the cellulose of the wood into more useful form. But what these symbions digest is usually *pure cellulose*, as is well illustrated by the symbiotic Infusorians (Trichonympha, etc.) in termites; and this is against our suggestion. The fact remains that in some cases of mycorhiza there is an indubitable increase in the protein-content of the roots after the fungoid infection has occurred.

The advantage to the internal fungus is least obvious in cases where the flowering plant is destitute of chlorophyll, as in the peculiar Bird's Nest Orchis (*Neottia nidus-avis*), Indian Pipes (Monotropa), and the rootless Coral-root (Corallorhiza), where the mycorhiza is in the rhizome. The first of these plants, if not the others as well, seems to have relapsed into complete saprophytism or absorption of decaying organic matter in the soil; and it is difficult to say why the fungus should not do this sufficiently for itself, as indeed so many fungi do.

Perhaps we get some light from experiments, still few in number, which indicate that certain internal fungi are able to fix atmospheric nitrogen. This has been proved for the fungus of the orchid Podocarpus and of some heaths. More facts must be established, but in the meantime it seems safe to suspect that one of the ways in which mycorhizal fungi may help their flowering partner is by fixing free nitrogen.

The remarkable symbiosis in the common heather has been well worked out by Miss Rayner. This characteristic plant of the moorland, which flourishes in the unready soil where little else will grow,

succeeds because it is a firm, not a single plant. The whole system of the plant is interpenetrated with fungus threads, which extend from root to stem, from leaves to flower, and rest against the envelopes of the seed, at hand to infect the next generation. Sterilised seeds will germinate and put forth a couple of leaves. But there the seedling stops without even developing roots. It is probable that the fungus is able to capture atmospheric nitrogen. A similar partnership occurs in some other Ericaceæ. It must be noticed, however, that Miss Rayner's careful conclusions must be reconsidered, by herself first of all, in the light of Knudson's recent criticisms.

Of great practical importance is the symbiosis between certain microbes (*Bacillus radicicola*) and plants belonging to the order Leguminosæ. The motile rodlet-like bacteria have a widespread occurrence in the soil, and enter the roots by the root-hairs. They develop into minute gelatinous threads (zooglœa) consisting of numerous bacteria, and these spread into the outer cells of the root. There they get free from the gelatinous cord, and in the abundant food they change from rodlets into forked or branched shapes, which in other bacteria are generally regarded as degenerative. The outer cells of the root are stimulated to form galls or tubercles, which are often the size of peas. The bacteria are benefited, for they feed on the abundant carbohydrate reserves in the root; and the green plants are benefited, for their partners are able to fix the free atmospheric nitrogen, some compound of which is eventually absorbed by the green plant. The evidence of this is now manifold: the Leguminous plant increases in nitrogenous compounds far beyond what can be accounted for by the mineral composition of the soil; in sterilised soil no tubercles are formed and the plants do not grow vigorously; the fixation of atmospheric nitrogen by *B. radicicola* and some others has been experimentally demonstrated.

The story reads like the conversion of a parasite into a symbion. When the bacilli first enter the plant, they multiply rapidly and show great vigour, and they produce some disorganisation in the cells of the root, from which they are absorbing carbohydrate material. But the plant soon recovers itself, being enriched by the nitrogenous compounds which the bacilli are providing. Soon, however, the bacilli become inert, and eventually they decay, leaving more nitrogenous material at the disposal of the green plant. An individual tubercle lasts only for a year; and if the Leguminous plant is more than an annual, there must be fresh infection of new rootlets. It is probably from the air dissolved in the absorbed soil-water that the bacilli obtain the free nitrogen with which they start, and it has been shown that the nitrogen-fixation is facilitated by an abundance of sugar and hindered by an abundance of nitrates or of proteins. What the bacilli do is not to be confused with the rôle of other soil-bacteria, e.g. Nitrosomonas, which oxidise ammonia

(from decaying organic matter), into nitrites; and of others, e.g. Nitrobacter, which oxidise nitrites into nitrates, the last forming an important part of the raw food-materials of ordinary green plants.

To get an adequate supply of nitrogenous material is one of the chief problems that plants have to solve, and it is interesting to recall some of the solutions. An ordinary green plant finds sufficient nitrates and the like in the average soil; the Bird's Nest Orchis, without chlorophyll, feeds as a saprophyte on the decaying organic matter in the soil; the dodder absorbs nitrogenous carbon-compounds from the clover or some other victim; the carnivorous plants have come to depend in part or mainly on the insects they catch; many forest trees are helped by their absorbent mycorhiza; but subtlest of all is the symbiosis between Leguminous plants and their root-tubercle bacilli. As Macgregor Skene puts it in his vivid *Common Plants* (1921): "Any plant trying to grow in the bare places of the earth is severely handicapped, if it has not at its disposal some special means of overcoming the prevailing nitrogen-hunger. Thus it is (by symbiosis) that the lupin can grow on the barren shingle, that the whin can conquer the heath, the broom the roadside, the rest-harrow the dune. In stations where other plants are hard pressed and are habitually stunted, these luxuriate."

PARASITIC PLANTS

Parasitism in general has been already dealt with somewhat fully, and parasitism among animals in particular, but it may be instructive to consider parasitic plants by themselves. We have included them here since parasites illustrate a mode of life in which advantage is taken of other organisms. As we have noticed, it is part of the definition of a true parasite (1) that it obtains some or all of its sustenance, as well as shelter and support, from its host; (2) that it does not confer any appreciable benefit; and (3) that it does in some measure escape from energetic activity by evading the more strenuous forms of the struggle for existence. To this it may be added that a parasite does not normally kill its host, which would be suicidal. In many cases it does not even weaken it appreciably. And, since there are no hard-and-fast lines, we may also admit that the parasite occasionally stimulates its host, e.g. to produce extra nourishment for its guest.

We have here chiefly to do with plants parasitic on plants, but the occurrence of plants parasitic on or in animals must not be forgotten. The most important are, of course, the bacteria which cause serious diseases in man, e.g. cholera and plague, or in his stock, e.g. swine fever and tuberculosis. A number of animals are attacked by moulds, especially when they lose their normal vigour, as may be verified in

the Empusa of moribund house-flies at the end of summer, or in the Saprolegnia mould which follows certain Bacteria in attacking weakened salmon. Very well known is the extraordinary fungoid fructification which grows out from certain caterpillars, projecting in front for several inches. The caterpillar is eventually killed by the fungus, and the dead larvæ, plus their stick-like projection, form one of the most celebrated Chinese medicines. There are many insect-fungoid linkages in the Laboulbeniales order of fungi.

Since the parasitic mode of life evades or circumvents the intensity of the struggle for existence by exploiting other organisms, it is not surprising to find many grades in the dependence of the plant parasite on its host. Thus there are some that are altogether dependent on a host, such as the mistletoe, the dodder, and Rafflesia. These are never seen living independently; they are *obligatory* parasites. But while many of the fungi, e.g. rusts, that attack living trees cannot be grown on a non-living substratum, there are others, e.g. most Ascomycetes, which can also flourish as saprophytes. To these the term *facultative* is applied.

But among the parasites that are always parasites, a useful distinction may be drawn between (*a*) those that are altogether dependent on the host—for water, for salts, and for already elaborated food—as in the giant-flowering Rafflesias, which have lost roots, stem, and leaves; and (*b*) those which retain their chlorophyll, like the mistletoes, and require only water and salts from their host. Other grades have been defined, but it is more important for our present purpose to emphasise the idea of the incipient parasite as a plant in difficulties, groping to discover some new mode of life and reaching it in various degrees of adaptation.

MISTLETOES.—The common mistletoe (*Viscum album*) may serve as a type of the family Loranthaceæ, which includes among its thousand species various grades of semi-parasitism. It grows on a great variety of trees, and within our common species there seem to be three different races, each linked on to a particular type of tree. Thus, in Britain, the mistletoe favours trees with broadish leaves, such as apple and poplar. Contradicting a widespread impression, it is least common on the oak; indeed, according to Macgregor Skene, there are only about a score of mistletoe oaks in Britain. On the Continent there is a mistletoe race on pines and another on fir-trees. It would be interesting to inquire experimentally whether there is something in the constitution of the pine-mistletoe which prevents its growing on the fir; or whether the structural differences in the three races of *V. album* are in part at least modificational, that is to say, directly evoked, or even *induced*, by the peculiarities of what we may almost call their "soils".

The winter-ripening fruit of the mistletoe is eaten by the missel-thrush; and when the swallowing is ineffective and the seed with its

sticky pulp adheres to the outside of the bill, the bird wipes it off on a branch. No doubt the seeds of the berries that are swallowed may be voided from the food canal, and there is a Californian mistletoe that jerks its seed out with explosive violence, but the roundabout distribution effected by the missel-thrush is typical.

The drying of the gluey threads of the fruit-pulp draws the seed close to the rough surface of the bark and germination begins in the spring or early summer. Out of the seed there grows a minute process which is usually regarded, not as a root, but as a stump of seedling stem. In any case, it is indifferent to gravity (a-geotropic) and it grows away from light (negatively heliotropic), and it broadens out into a minute attaching disc. From this there grow out two or three cortical roots which spread up and down in the bark. From each of these a sucker sinks through the bark, at right angles to the surface, and continues until it reaches the cambium, where it stops. Nothing more happens that first year.

In the next season the suckers send outgrowths up and down the cambium just outside the wood, and from the wood they absorb water and salts. They never grow round the branch, which would tend to strangling; they are not embedded by the increase of the wood, for the elongation of the suckers keeps pace with the formation of new wood. It is in the summer of the year after the sprouting that the young mistletoe develops its first pair of leaves, and later on there are branches as well. Moreover, the outgrowths which extend up and down the branches of the host produce buds which emerge on the surface. From these there may arise new mistletoe bushes, fixed to the branch at some distance from the original parasite. It may be noted that the characteristic bushy growth of the mistletoe, spreading out on all sides, is associated with the plant's indifference to the gravitational stimulus; this mode of branching obviously works better than an entirely vertical growth.

Some of the mistletoes differ in details from the type we have described. Thus in the genus Loranthus attachment is effected by a broad attaching surface, and sometimes by a radiating growth, the "wood-rose" of some Mexican mistletoes. In *Loranthus europæus* the absorbing outgrowths show at intervals little swellings which suggest secondary reservoirs for the watery sap. At every turn we find what may be interpreted as adaptations. Thus the leathery character of the leaves in the common mistletoe lessens the loss of water by transpiration, and some other species go much further in this xerophytic direction, notably the quite leafless mistletoe found on juniper bushes in some dry Mediterranean regions. In this last case the photosynthesis must be effected by the pale-green twigs. In this connection Neger calls attention to a very interesting instance of "convergence", that is to say, similarity of structure and habit in forms which are not very nearly related. The leafless *L. aphyllus*

is a parasite on South American cactuses of the genus Cereus, plants remarkably well adapted to making the most of the scanty water-supply in deserts. Now in South Africa there is another leafless mistletoe, *Viscum minimum*, which grows on a spurge, *Euphorbia polygona*, that bears a very close resemblance to the unrelated cactus!

In his luminous essay on Parasitic Plants (1926) Macgregor Skene makes an instructive comparison between the growth of the mistletoe on an apple-tree and the growth of a scion on its stock, say, of a pippin on a crab-apple. The differences are perhaps greater than the resemblances. A mistletoe cannot be grafted on a host; it must establish the linkage in its own way. Grafting is successful only when scion and stock are nearly related, e.g. apple and pear; but the mistletoe grows on an unrelated tree. The scion must get the requisite water and salts from its stock, but it gives back organic food; the mistletoe gives back nothing. "The experiment has been made of growing a mistletoe on a young apple-tree and, when it was fully established, of removing all the apple foliage. For a year the union subsisted, and then the apple died from starvation and with it the mistletoe."

THE DODDER.—In contrast to the mistletoes, and doubtless arising in a very different way, are the dodders (Cuscuta), in which there is no chlorophyll. They are related to the Bindweeds, and are to be thought of as climbers which have become parasites. A reddish British species is found growing in a tangle with ling and thyme; another of a yellowish colour victimises clover and flax. It often deserves its German name of "devil's twine". The foliage is represented by a few minute scales, corresponding to leaves reduced almost to vanishing point. Except in the seedling there is no root. But the long stem has both activity and specialisation, and at frequent intervals it bears clusters of small bell-like flowers.

The seeds of the clover's dodder fall to the ground in autumn, or they may be sown along with those of the harvested crop. In either case they do not germinate till there are young clover plants rising from the ground. Out of the seed there emerges a slender yellow thread, an inch or two in length, with a vestigial root at one end and a mobile shoot at the other. The root end may absorb water, but it does not enter the ground; the other end grows at its own expense, shrivelling behind, and it nutates like a twining plant. It levers itself on the ground as if it were a little threadworm seeking for a host. It sometimes survives about a month of starvation. If it touches a clover stem, it twines round it, making several close coils, from the inner surface of which there grow small suckers or haustoria, penetrating into the bast-tissue of the host. In this way the young dodder gets materials for further growth, and it begins to branch. Loose coils are formed round the stems and leaf-stalks of the clover,

quite different from the close coils, which are like those of a tendril. There is usually an alternation of close coils and loose coils.

Since the root of the seedling is a transient vestige, the stem-suckers of the dodder absorb soil-water from the sap-wood elements of the host. Since the foliage of the dodder is represented only by minute scales, and since chlorophyll is wholly or almost wholly absent, there can be little or no photosynthesis, and there is an absorption of carbohydrates (especially glucose) from the host; and probably of proteins as well, for the "sieve-tubes" of the two plants are in contact. Cross-sections show that the tissues of the parasite come into intimate union with similar tissues of the host, wood with wood, and bast with bast. Indeed, it is sometimes difficult to detect the boundary-line. The suckers produce ferments which can digest not only the starch, but the cell-walls of the host.

Peirce has noticed that if a dodder plant be prevented from forming close coils and suckers, it may develop an appreciable quantity of chlorophyll—enough to keep it alive! The same slight greening has been observed in dodders grown in the shade or on weakened hosts. Another interesting experimental fact is that *Cuscuta monogyna* has been grown to maturity without a host at all, in a culture of glucose solution.

The habits of dodders are repeated in tropical countries by species of Cassytha, but these belong to the Laurels, not to the Bindweeds—an interesting evidence of the independent origin of the same adaptations in unrelated plants. In the Cassythas there is the same twofold absorption of watery and elaborated sap; and they also illustrate like dodder a change from yellow to greenish when grown in the shade.

ROOT-PARASITES.—About the base of broom-plants and whins we occasionally find a remarkable parasite—the broom-rape (Orobanche). A brownish fleshy stem stands upright for a foot or more, bearing scales and numerous dull-coloured flowers. There is no chlorophyll, and the organic food is obtained by sending numerous suckers into the roots of the broom. There is a very intimate union of the root-tissues of parasite and host. An interesting feature, also illustrated by some other root-parasites, is that the wind-borne seeds, which are very numerous and very minute, will not germinate except in actual contact with the roots of an appropriate plant. As some kinds of Orobanche are restricted to one host, and none have many alternatives, we can understand that variations in the direction of abundant and minute seeds would be favoured in the course of Natural Selection.

Another striking root-parasite is the Toothwort (*Lathræa squamaria*), at home on the hazel. The underground stem is covered with fleshy tooth-like leaves, each bent on itself so as to form a cavity with a narrow slit-like opening. In this cavity there are numerous

minute glands (hydathodes), which probably get rid of surplus water and keep a sap-current agoing, for an above-ground foliage is represented only by scales on the purplish upright flower-stalk. As there is no chlorophyll the organic food is entirely obtained, as in the broom-rape, from the roots of the host-plant. This is another of the cases in which the seeds will not germinate unless they are brought into contact with the roots of the appropriate host.

In those tropical countries in which conditions favour vegetative exuberance, there is, partly because of the luxuriance, a frequent overcrowding and an intense competition. Hence also the frequency of particular adaptations such as climbing and such as root-parasitism. The latter finds abundant illustration in the family Balanophoreæ, often gorgeous in flower colouring, and large in size though with reduced foliage. The only European representative is *Cynomorium coccineum*, which is found in southern countries as a root-parasite on Pistacia and myrtle. In this family the union of parasite and host is marked by tuberlike swellings in which the tissues of the two plants come into very intimate union.

In another family, that of the Rafflesias, the parasitism goes even further, for the tropical species have lost not only leaves and chlorophyll, but the roots and the stem itself. From the seedling there develops a hollow fibrous cylinder which embraces the stem and root of the host—often a vine—and gives origin to an internal web of absorbing filaments. In some cases, e.g. Pilostyles, these suctorial threads suggest the hyphæ of a fungus, and, as Neger aptly says, the parasite has sunk, as regards its vegetative system, from the level of an ordinary flowering plant to that of a Thallophyte! But the flowering system suffers no degeneration. From the hidden filaments there grow flower-buds which burst through the host's bark or root-cortex and develop extraordinarily. In a famous species, *Rafflesia arnoldii*, the flower is blood-red in colour, with a carrion stench, and a diameter of about a yard—easily the largest of known blooms. The only European representative of the order of Rafflesias is the Mediterranean *Cytinus hypocistis*, whose puzzling flower-buds burst through the ground from the roots of a shrubby rock-rose (Cistus), and develop into "a flowering spike of scarlet scales and yellow flowers".

It is interesting to notice that dodders, broom-rapes, Balanophoras and Rafflesias belong to different orders of flowering plants; for this shows how the same way of living and somewhat similar adaptations may evolve independently from different origins.

We have kept by themselves the partial root-parasites, such as eyebrights (Euphrasia), yellow-rattles (Rhinanthus), and cow-wheats (Melampyrum), which retain their chlorophyll and their leaves, but have their roots intimately fastened to those of grasses and herbs, from which they absorb elaborated food. Many plants which

cannot be called actual parasites seem to take advantage of the roots of their neighbours into which they may become almost accidentally pressed. They use their opportunity, and from such a beginning there is a gradation to eyebrights, which profit by such a union, and thence to cow-wheats which cannot do without the outside help. Beyond this is the interesting case of the Alpine Tozzia, a relative of the Eyebright, which spends the first year of its life as an underground parasite and sends up in the second year a flower-stalk with rather fleshy yellowish-green leaves. But even when it gets its foliage it remains dependent on its hosts. Here it is interesting to note that while the seeds of ordinary Euphrasias can germinate in any soil, those of *Tozzia alpina* must begin in contact with the root of an appropriate host.

ORIGIN OF PLANT PARASITES.—Following Neger's scholarly discussion of this problem in his *Biologie der Pflanzen* (1913), we may distinguish the following possibilities. (1) Parasitism may be the outcome of an epiphytic habit, as is well-illustrated by the gradations among lichens. Some are epiphytes and nothing more; others show different degrees of parasitism, in addition to their own intrinsic symbiosis. It is probable that the mistletoes may also have originated from epiphytic ancestors; indeed, half a dozen or so out of a thousand species are still epiphytes. (2) Parasitism may also have evolved from saprophytes, as is forcibly suggested by many of the Fungi, which pass from the absorption of decaying organic matter to prey upon living tissues. A familiar example is *Botrytis cinerea*, a fungus-pest of damp hothouses. As Neger says: Nowhere more than in the plant world is it true that "L'appetit vient en mangeant". (3) The story of the dodders points to the possible origin of parasitism from the climbing habit. The fact that *Cuscuta gronowii* sends its attaching organs into dead supports is not without significance. (4) Another mode of origin may have been from a mutually beneficial partnership of a more or less external sort, e.g. between the roots of two adjacent plants, both able to live independently. From more intimate partnership, such as external and internal root-fungi (mycorhiza), parasitism may sometimes have resulted, when the fungus became too strong for the other plant, or when a plant which once had chlorophyll, like the Bird's Nest Orchis, became entirely dependent on its mycorhiza. Some interesting experiments have been made in the way of artificially inducing temporary partial parasitism, e.g. of a vine on a cactus. These unions are to be distinguished from ordinary grafting, which only succeeds when scion and stock are nearly related. Yet it is difficult in life's intricate inter-relations to enforce logical distinctions, for a pea has been induced to become a partial parasite of a bean, and even blossom on its bearer!

Parasitism among plants is even more diverse in its forms and gradations than among animals; and its variety brings home to us the idea that degeneration is not always the nemesis of becoming dependent on another organism for sustenance. No one can call a partial parasite like the mistletoe a degenerate plant, yet it is entirely dependent on its host. Even in regard to cases like dodder, where the leaves have gone, there is considerable floral exuberance, produced it is true at another's expense. In an extreme case like Rafflesia, sans leaves, sans stem, sans roots, we must give the plant credit for a superlative flower. In many parasitic plants there is marked reduction of parts, but against that there has to be reckoned the development of special adaptations, such as haustoria.

There is another point, that we be careful not to put the cart before the horse in interpreting the reduction of parts and qualities in some parasitic plants. For the beginning of reduction and weakness may be seen in some plants that are in no way parasitic, and such a reduction might make an incipiently parasitic mode of life highly advantageous. Thus, as Skene points out, golden-leaved varieties are not uncommon among cultivated plants, and indicate a deficiency of chlorophyll which would be fatal in natural conditions, unless indeed the plant took or had begun to take to, say, root-parasitism. We have referred to the yellowish colour of Tozzia, the Alpine relative of our eyebright, and "we may look on Tozzia as the first step in the process of reduction".

We mean that some weakness, such as chlorophyll-deficiency or leaf-reduction, may be a precondition of parasitism. That is to say, if opportunity is offered to these incipiently weakly plants—and opportunities of root-parasitism seem to be frequent—a variation in the direction of parasitism may have immediate survival value. Is not reduction as likely to be the cause of parasitism as parasitism of reduction?

ECOLOGY OF PLANT REPRODUCTION

The merely outline survey here attempted has to do with the Natural History of reproduction in plants, and in particular with pollination and seed-dispersal.

There are four main modes of multiplication in the plant world.

(*a*) The simplest of all is seen when a unicellular Alga or fungus divides into two units which then go apart. Not far removed from this is the budding of a unicellular organism such as a yeast-plant, or the rapid division within the cell wall or a special cyst, the result being to form "spore-cells" which have the advantage of being motile in some cases, or of being very resistant (to drought, etc.) in other cases.

(*b*) On a second grade may be grouped all those cases where multicellular plants multiply vegetatively, without specialised reproductive cells, and therefore without involving any process comparable to fertilisation. Thus a mould may spread by means of rapidly growing, easily broken, threads (mycelial hyphæ) over a saucer of paste, or over the grass on the links, there forming "fairy rings" by dying away internally as they extend externally. At a higher level there may be multiplication by breakage of the long-branched protonema threads which develop from the spores of mosses; and very frequent is the multiplication of liverworts by means of buds or gemmæ, of which there is a gradation from one-celled to many-celled forms. We have noticed elsewhere the peculiar case of the soredia of lichens. Many plants which have specialised sex-cells or less specialised spore-cells may also retain a capacity for vegetative multiplication in natural conditions, as is illustrated by the duckweeds (the minutest of Flowering Plants), or by the bulbils that fall from the axils of the Tiger Lily. The most obvious limitation to reproduction by means of detached pieces is that the range of dispersal is not likely to be great, whereas spores and seeds, being either minute or specially adapted, can be carried for great distances by the wind, by water-currents, and by animals.

(*c*) The third mode of multiplication in plants is by means of special reproductive units, which may or may not require fertilisation. When the unit does not require fertilisation, it is called a spore; but it is obviously difficult to draw a firm line between this and a unicellular gemma, as seen, for instance, in some liverworts. Moreover, in most cases the life-story is complicated, as in Liverworts, Mosses, Ferns, Horsetails, and higher plants, by the occurrence of two generations—one, the *sporophyte*, producing germ-cells (spores) which do not require fertilisation; and the other, the *gametophyte*, producing dimorphic germ-cells (egg-cells and sperm-cells) in which fertilisation must occur.

It seems clearest to rank multicellular plants that multiply by spores not requiring fertilisation along with those whose dimorphic spores are definitely sex-cells and require fertilisation. For (1) there is a deep difference between multiplication by spores and multiplication by means of detached vegetative pieces, like gemmæ; (2) among the Algæ there is often a fusion of spores (e.g. Ulothrix), although it is not possible to distinguish the one as male and the other as female; and yet in other Algæ (e.g. Fucus), the dimorphism is pronounced, and the one set must be called egg-cells and the other sperm-cells; (3) there is a gradation between (*a*) independent spores, (*b*) uniform spores that unite in pairs (isogamy), (*c*) dimorphic spores that develop into two kinds of gametophytes (male and female), and (*d*) those that develop into one kind of gametophyte (with both male and female organs). In a typical non-seeding higher

type, such as a fern, the strong vegetative plant (the sporophyte) produces spores which are all alike (isogamous). They fall to the ground and in favourable conditions each may develop into a small and delicate prothallus (gametophyte), which bears sexual reproductive organs (archegonium and antheridium, or ovary and spermary). An egg-cell in the archegonium is fertilised by a sperm-cell from the antheridium, and develops into a young sporophyte. This is the typical alternation of generations, which is discussed elsewhere.

(*d*) It is elsewhere explained that in the seed-bearing plants, from the old-fashioned Cycads to the Conifers, and from these to the Phanerogams with their true flowers, there is a persistent, though much masked, alternation of generations. But from the ecological point of view it is desirable to keep the seed-bearing plants in a group by themselves. For this there are two reasons, first, because of the practical suppression of the gametophyte generation as a separate phase; and second, because what is separated from the maternal plant, or from the female portion of the parental plant, is a *seed*, which is already a young plant (an arrested sporophyte) that has been living for some time in dependence on the parent, and is liberated in a manner comparable ecologically to the viviparity of mammals. From the standpoint of comparative embryology, the flowering plant shows alternation of generations with a much reduced gametophyte stage; but the development, equipment, and dispersal of the seed is so *unique* that the separation of seed-plants from all others is warranted as an ecological convenience.

ECOLOGY OF THE FLOWER.—Morphologically, as Goethe and others recognised at the end of the eighteenth century, the flower is a shortened region of the plant-axis, bearing a number of transformed foliar organs, some of which (stamens and carpels) are specialised as spore-producers. Typically there are four whorls, tiers, or series of floral structures, all of which are homologous with leaves: the sepals (forming the calyx), the petals (forming the corolla), the stamens (forming the andrœcium), and the carpels (forming the gynœcium or pistil).

Physiologically regarded, the flower is the reproductive part of a seed-plant, the stamens producing microspores, which give rise to pollen grains, and the carpels producing macrospores (or megaspores), each known as an embryo-sac. A male nucleus arises within the pollen-grain or within its outgrowth the pollen-tube, which actually represents the much-reduced male gametophyte. A female nucleus arises within the embryo-sac, which actually represents the much-reduced female gametophyte. The union of the two gametes forms a zygote, which proceeds to develop into a young sporophyte, the embryo plant within the ovule. It is no longer regarded as strictly accurate to speak of the stamens as male organs and of the

carpels as female organs, they are sporophyls specialised to produce microspores and macrospores; but the flower is more clearly than ever the reproductive part of the plant.

Ecologically regarded, the flower is that part of the seed-plant that makes the reproduction more secure by establishing certain environmental inter-relations. Thus it is plainly an ecological fact that the majority of flowers attract insect visitors which make sure work of cross-pollination; and it is another ecological fact that many fruits are attractive to birds which scatter the undigested seeds. Let us begin with pollination.

POLLINATION.—In ancient times it was known, though very vaguely understood, that a male floral spike of the Date Palm should be hung over a female floral spike if the fruit was to form aright; but it was not till near the end of the seventeenth century that Camerarius demonstrated that in ordinary flowering plants pollination is necessary if fertile seeds are to be formed. Pollination is the actual deposition of the pollen-grain on the stigma of the pistil, and it leads to the downgrowth of a pollen-tube into the style, towards the ovule in the ovary. A male nucleus in the pollen-tube enters into intimate union with the female nucleus (or egg-cell) inside the embryo-sac of the ovule; and this is *fertilisation*—the beginning of a new individual life. As the result of fertilisation an embryo is formed in the seed.

As the great majority of flowers have stamens producing pollen, and carpels producing egg-cells, and as these are in close proximity, nothing seems more natural than self-pollination or autogamy. In the strict sense this means that the pollen of a stamen may serve to pollinate the stigma of the same flower; and this eventually amounts to what is called self-fertilisation in animals like the liver-fluke and the tapeworm. But, as a matter of fact, this autogamy is very rare; for in many cases the stamens and the carpels of one and the same flower are not ripe at the same time, and in other cases there are mechanical reasons hindering the autogamy. But while self-pollination is relatively rare, its occurrence has been observed in some common flowers, such as Geranium, Willow-herb, and Enchanter's Nightshade, and it is notably frequent in flowers living in Alpine or Arctic habitats where insects are scarce.

In some flowering plants there is a strange arrest of development in the flowers, which fail to open and often remain underground. They necessarily show self-pollination. Such flowers, called cleistogamous, often occur very early or very late in the year; and they have the advantage of being well-protected from rain and from intruders, and in having their seeds self-sown. Cleistogamy occurs constantly in the subterranean flowers of the fragrant violet and the milkwort; it occurs occasionally in Dead Nettles, Wood Sorrels,

Rock Rose, and Balsam. In a few cases, like the Bee Orchis (*Ophrys apifera*), *all* the flowers are cleistogamous. The intimacy of the self-fertilisation may be inferred from the fact that in some cases, like sorrel and balsam, the anthers of the stamens do not split, and the pollen-tube has to grow out of the anther into the pistil. In many cases there is a great reduction in the carpels, e.g. the absence of a stigma, and a great reduction in the number of the stamens. This peculiar occurrence of closed self-pollinating flowers may be regarded as an arrest of development—a *time-variation*—in conditions of unusual difficulty.

It should be noted that autogamy does not necessarily mean that the flower itself effects the deposition of its own pollen on its own stigma, for that may be effected by insects within the flower. The well-known Yucca-moth, Pronuba, seems often to pollinate a stigma of the Yucca flower with a ball of pollen collected *from the same bloom*; but sometimes the pollen is carried from another Yucca plant, and that is what is meant by cross-pollination. Intermediate between the two, but nearer autogamy, are cases where the pollen is brought from another flower *of the same plant*. The Yucca-moth may be an agent in all the three modes of pollination—within the same flower, within the same inflorescence, or from one Yucca plant to another!

WIND POLLINATION.—In many conifers, like the pines, and in catkin-bearing trees, such as birches and poplars, and also in many grasses, the pollen is carried from plant to plant by the wind. In such cases it is common to find one or more of the following adaptations:—mobile inflorescences easily shaken by the wind; very open and simple flowers which are often ripe before there is much foliage; delicate filaments to the stamens so that the anthers (occasionally explosive, as in nettles) are readily jostled in the breeze; abundant pollen, except in some of the grasses and sedges; dry pollen grains (sometimes with wings, as in pines); and plumose stigmas which expose a large surface for pollen capture. Many wind-pollinated plants, such as oak-trees and grasses, are conspicuously successful, but perhaps there is no correlation between the two facts. There seems not a little wastefulness and fortuity in wind-pollination; yet it is well suited for plants with primitive or slightly developed petals and sepals, and for those whose flowers appear early in the year, before there are many insects about. Self-pollination is often avoided in wind-pollinated and in other flowers by the fact (dichogamy) that the stamens and pistil are not ripe in the same flower at the same time. The protandrous condition, when the stamens are ripe first, is illustrated by Campanulas, Composites, Labiates, Umbellifers, etc.; the protogynous condition, when the pistil is ripe first, is illustrated by Foxtail Grass, Sedges, Figs, Hellebore, Hops, etc.

WATER POLLINATION.—Some peculiar features are exhibited by aquatic plants. Thus in the sea-grass (Zostera), the pollen-grains are peculiar in being long filaments, and the stigma is also filamentous. The pollen-threads have the same specific gravity as the sea-water and can float at any level. This elongation of the pollen-grains occurs in not a few aquatic plants. In Najas the female flowers are near the bottom, and the very much simplified male flowers are nearer the surface. The pollen-grains are almost spherical and so heavily weighted with starch grains that they sink when they are shed and are thus caught on the lower female flowers.

The tape-grass Vallisneria is an interesting example of those water plants in which the pollination is effected at the surface. The male flowers are low down on a spike enclosed in a spathe; the female flowers are solitary and float when ripe on the surface on the end of long slender stalks. When the male flowers are ripe, the inflorescence breaks off, floats up to the surface, and sets the individual florets free. They drift about passively and sometimes collide with a female flower, transferring to the pistil a little clump of coherent pollen-grains. After pollination there is a remarkable spiral coiling of the stalk of the female flower, which brings the fruit to the bottom, where it ripens. In the American Pondweed (Elodea) there is a somewhat similar sequence; but in this case it is the great elongation of the ovary that brings the female flower to the surface, where pollination occurs. This plant was brought from America to Britain in 1842, and has become over-abundant in many canals and rivers in Europe. As no male flowers occur in the Old World, the multiplication must be purely vegetative. It is effected by the breaking off of twigs.

POLLINATION BY INSECTS.—We have mentioned Camerarius (1665–1721), who proved experimentally that fertile seeds cannot be formed without the co-operation of pollen, and also insisted that the anthers and the ovaries were the male and the female sex-organs of the flower in no figurative sense. This conclusion was confirmed and deepened by Kœlreuter (1733–1806), who discerned that genuine, i.e. animal-like, fertilisation must occur in flowering plants, and made many important experiments in hybridisation. As he also recognised the rôle of insects in carrying pollen and the use of nectar as an inducement to the insects to visit the flowers, he leads us naturally to Sprengel, who linked him to Darwin.

Christian Konrad Sprengel (1750–1816) was a keen observer of the inter-relations between flowers and insects. In his *Newly Discovered Secret of Nature in the Structure and Fertilisation of Flowers* he expounded three conclusions: (1) that many of the characteristics of flowers, such as nectaries, markings, and shapes, are adaptive to the visits of insects which secure cross-pollination;

(2) that cross-pollination is the rule, not the exception, there being many arrangements which effectively hinder self-pollination, or make it unlikely; (3) that one of these is dichogamy, or the ripening of the stamens and carpels of a particular flower at different times. Subsequent experiments by Andrew Knight, William Herbert, and especially K. F. Gartner disclosed the fact or probability, which Sprengel had missed, that cross-pollination gives better results than self-pollination as regards the number and the vigour of the seeds —a conclusion which Darwin was not slow to use in support of his theory that the adaptations ensuring cross-fertilisation are the outcome of a long-continued process of Natural Selection.

Patient and precise observations, well illustrated by the work of Hermann Müller, have shown that many kinds of flowers are visited by particular insects, which unconsciously effect cross-pollination. The most important of these pollinating insects belong to the following orders:—Hymenoptera (e.g. bees), Lepidoptera (butterflies and moths), Diptera (two-winged flies), and Coleoptera (beetles); and the relation between the length of the insect's "tongue" (a suctorial specialisation of diverse mouth-parts) and the depth of the nectary is the most decisive fact in determining the success of the visits, both to the insects and to the flowers. The insects usually seek out the flowers for the sake of the nectar and the pollen, but in most cases for one or the other. Thus hive-bees, which use both as food, are usually pollen-collectors at one time and nectar-collectors at another. It is an interesting detail that when a successful worker-bee has filled her honey-sac and returned to the hive and emptied it, she executes on the comb a peculiar excited dance, which is different from that in which she similarly indulges when her treasure-trove has consisted of pollen only.

Of much ecological importance is the general fact, often verified since first stated by Aristotle, that a hive-bee is for a time constant to one kind of flower. If she has found white clover profitable, she will keep to white clover; and, what is more, some of her sister-workers, taking their olfactory cue from her, will also search for white clover as long as the supplies last. But next day it may be another kind of plant that is visited. The same holds for some other insects, and in many cases a particular insect visits only a few kinds of flowers. To the plant this is advantageous, since effective pollination is more secure when the insect visitor is adapted and habituated to a particular type of blossom. It is probably economical to the insect; and in the case of hive-bees it obviates unnecessary mixing of different kinds of honey in the same cell of the comb. At the same time it must be noted that the so-called "constancy" of bees' visits to particular species is not more than a general rule. To those who know bees it is now a postulate that there is nothing that bees "always do". For they are individualities!

In spite of many experiments there remains much difference of opinion as to the rôle of the various qualities of flowers in attracting insect visitors. There seems to be, as should be expected, considerable diversity among the different types of insects, some being more susceptible to colour and others to fragrance. To begin with, there is often some experimenting on the insect's part, as has been noticed in regard to newly introduced garden-flowers not previously tried. The insects try and try again, and they sometimes enregister their experience; as has been proved when humble-bees have discovered how to bite a short-cut into the nectary of a new and difficult bloom, and at once do so when they reach another flower of the same kind.

In the course of many tentative visits, some successful and others disappointing, the insects establish associations (to express it psychologically) or conditioned reflexes (to express it physiologically); and these may be based on odours, brilliance, colour, and form, to put them in their probable order of importance. Many insects live in a smell-world, even more than dogs do, and may have thousands of olfactory bristles, disposed at strategic points on their body, on the antennæ in particular. When a successful worker-bee executes her "honey dance" on the comb, the bystanders rush forward to nose her, thus discovering a clue to the kind of blossom that it would be profitable for them to search for. They do not, of course, reflect over their behaviour, but it has been proved by Frisch that in a few minutes they may discover the very patch of flowers where the first bee—still in the hive—filled her honey-sac. When a worker-bee finds a highly profitable flower she sometimes emits a little odoriferous spray from a posterior gland, and this bee-odour on the plant may be an olfactory cue useful to other bees, especially if the treasure-trove be in itself scentless. The secretion of the odoriferous gland is sometimes used as a signal in the confusion of swarming, or when there is some difficulty in the return to the hive. There also seems to be a characteristic queen-scent, the absence of which may be rapidly detected by the workers of a hive which has lost its queen. There is no doubt that scent counts for much in the life of bees and many other insects; and there is thus good reason for attaching importance to the experimentally verified conclusion that the specific odour of flowers serves as a basis for association-forming. But this must not lead us to forget the prior physiological question as to the primary significance of odours in the plant's biochemical routine.

It has been proved by experiments, beginning with Lubbock's, that bees and some other insects can distinguish colours as colours, that is to say, apart from degrees of brilliance. When they have established an association between a particular colour and a satisfactory meal, they will pick out that particular colour from among

others and give it the first trial. They will do this repeatedly, even though the meal is not forthcoming. This proves a registration of colour as colour, but it has its limitations. Thus hive-bees seem to mix up colours that are near one another, such as yellow and orange, or blue and violet. Though they can see the ultra-violet rays that are invisible to us, they seem to be colour-blind to scarlet. Yet they may be attracted to a brilliant scarlet flower whose surface reflects much light, more than to a dull flower otherwise equal. To give flower-visiting insects credit for evolving the colours of flowers is credulous, but given physiological reasons for the presence of floral pigments, and some of these reasons are now becoming apparent, it is justifiable to say that bees and other colour-discriminating insects may have played a part, throughout the ages, in favouring flowers with certain colours and in eliminating others. It is unnecessary to use such words as "prefer"; what has been proved is that certain insects build up useful associations with particular colours, and more readily with these than with other colours. More experiments are necessary before we can say much as to *inborn* susceptibility to certain colours rather than to others.

To a less extent than odour and colour, the brilliance and the shape of flowers may be of importance in securing the visits of insects.

In warm countries, and very markedly in Java, pollination is sometimes effected by birds, such as humming-birds, sun-birds, and honey-suckers, which suck up the abundant and unusually fluid nectar. The list of habitual bird-pollinators, as dependent on the flowers as the flowers are on them, is already long, and it is rapidly growing. But while insects and birds are both important, other animals are trivial; snails occasionally carry pollen from blossom to blossom in their slow-going way, and Freycinetia is actually pollinated by bats.

ADVANTAGES OF CROSS-POLLINATION.—The frequency of cross-pollination and of arrangements that prevent self-pollination cannot be overlooked, but it is doubtful whether there is in the latter as such any deteriorative danger, or in the former any positive promotion of vigour or of variability. The results of experiment are strangely discrepant. Probably the most prolonged experiments are those on maize, which is naturally a cross-pollinated plant, but can be artificially self-pollinated. This has been studied for twelve or more successive generations, and the first results confirmed Darwin's general conclusion that self-pollination deteriorates vigour and productivity. Without there being any actual degeneration, the successive self-pollinated crops of maize plants showed reduction in size and productiveness, but only to a certain point, after which there was stability again, and a marked uniformity. There was, however, a sifting out into true-breeding sub-varieties marked by

differences in structural detail. Finally there was an appearance of "monstrosities", such as dwarfs, albinos, and forms with various grades of abortion in pollen and ovules. Apart from the monstrosities, which may also occur among cross-pollinated plants, the reduction in size, productivity, and variability was not associated with unhealthiness or degeneration in the majority. What happened was probably this. The inbreeding involved in the self-pollination tends to bring to light a number of recessive characters (see Mendelian Inheritance), which were kept out of sight by their corresponding dominants, which are more likely to be present when cross-pollination is the rule. The apparent bad effects of inbreeding (self-pollination) are in all probability mainly due to the segregation and unmasking of recessive characters, while the apparent stimulus following outbreeding (cross-pollination) is in all probability mainly due to the complementary action of pooled dominant factors.

It may be regarded as certain that established self-pollination does not necessarily imply loss of vigour or variability; and it should be remembered that the very successful and variable hawkweeds (Hieracium) are parthenogenetic!

DISPERSAL OF SEEDS.—It was towards the end of the Old Red Sandstone Period that Seed-bearing plants emerged, and it was a great step in Organic Evolution. Previously plants had multiplied by spores or unicellular germs, separated in vast numbers from the parent; but now there began to be multiplication by means of seeds. That is to say, what were liberated from the parent were embryo plants, in a resting stage of development, but more or less well-equipped; and they had been living for some time in intimate union with the parent plant. The contrast between multiplication by spores and multiplication by seeds was something approaching or anticipating the contrast between oviparous and viviparous animals. A mother salmon liberates thousands of eggs on the gravelly bed of the river; contrast that with the mother otter that gives birth in her retreat to a well-formed cub. So, in a broad way of speaking, do sporophytes differ from spermophytes, though, as has been explained elsewhere, the spermophytes are still disguised sporophytes.

A well-equipped seed's chances of life when it is sown are much greater than those of a spore, but there is the disadvantage attendant on a great advantage, that even the smallest seeds are large compared with spores; and it is therefore more difficult to secure their dispersal. What we seek to illustrate here is the diversity of ways in which the problem of seed-scattering has been solved.

Before doing so, let us make an elementary point clear, that for purposes of dispersal the seed and the fruit, especially when small

and dry, may be practically the same. The fruit is the ripe ovary or seed-box, often with the addition of accessory parts, such as the top of the floral axis. The seed is an embryonic plant in a state of arrested development, often equipped with food-material, and it lies within the seed-box. The anatomical distinction is clear, and yet it may be unimportant ecologically. Thus the familiar wind-borne fruit of the dandelion consists of a delicate filament with a nutlet at the base and a beautiful parachute of radiating hairs at the tip. What is lodged in a crevice of the soil is the nutlet fruit, which contains a single seed. Fruit and seed are in such cases practically identical. The same is true of other nutlet-fruits or achenes, such as those of grasses. Similarly there is a group of dry fruits (schizocarps) which do not open, as pods and capsules do, but divide into a number of pieces each with a single seed. In technical phrase they are indehiscent, yet they break into "merocarps", each usually with a single seed. The fruits of hemlock and of Labiates are of this type. What is sown is a piece of fruit, and when sprouting occurs the seedling has to find its way not only out of the softening seed-envelopes, but out of the decaying wall of the fruit-fragment.

The majority of fruits are included in the following five groups.

(1) The box fruits or capsules break open or dehisce to some extent when mature or moribund, and thus allow the seeds to escape. The simplest is a pea-pod or legume, consisting of a single folded carpel or sporophyll; the siliqua, characteristic of Crucifers, is built up of two carpels; the pansy fruit of three; and so on. Most complex are capsules like poppy-heads, where the dehiscence takes the form of a ring of little holes, through which the seeds tumble out. In many cases the lid of the capsule falls off when the seeds are ripe. The most important fact is that the dehiscence of the carpels is to be ranked beside the withering, wrinkling, and fall of foliage leaves, for carpels are transformed foliar organs.

(2) Schizocarps or "Splitters" are dry indehiscent fruits, like those of Umbelliferæ and Labiatæ, which divide into a number of pieces, each usually containing a single seed. The seeds do not escape from their fruit-enclosure, yet the fruit splits into pieces.

(3) A third group of dry fruits includes the true nuts, and nutlets technically called achenes. They do not open to liberate the seed, neither do they split into pieces. Indeed, they are usually single-seeded. A true nut is well illustrated by the hazel-nut, with a very hard fruit-wall to which the seed is not adherent. In the seed-like fruits of a buttercup the wall is not hard and the seed—not very difficult to pick out—lies freely within. In the grain of wheat, the fruit-wall is

rather leathery, and the seed adheres to it. In such cases fruit and seed are practically identical; what is sown is the fruit.

(4) Among the soft fruits there are two main types—the stone-fruits, like cherries and plums, and the true berries, like gooseberries and grapes. In stone-fruits, the hard part or "stone" is the third and innermost layer of the fruit, the endocarp, and the pulp is the middle layer or mesocarp. Inside the stone the familiar kernel is of course the seed. In true berries, on the other hand, the hard part is the wall of the seed; and the pulp of the fruit often contains several seeds. It is interesting, though not relevant to ecology, to think out some of the difficult fruits; thus it seems that a coco-nut is a stone-fruit in which the pulp is represented by the fibrous layer used in making mats; and that the walnut is a stone-fruit, for outside the familiar stone or nut there lies the firm, fleshy middle part corresponding to the juicy part of a peach.

(5) Berries are soft fruits without a hard endocarp (innermost fruit-wall), but with a hard coat round each of the seeds, which are embedded in the pulp. Even ecologically it is of some importance to understand clearly that the seed of a cherry, let us say, is inside the hard stone of the fruit, whereas the hard bodies inside a grape are the seeds, each with a very strong envelope. A gooseberry is a typical berry, but there are some difficult forms, such as oranges, with hard seeds embedded in the centre of a pulp composed of much enlarged juicy cells. Even more difficult is the date, where the seed inside the fleshy pulp has its own nutrient tissue (endosperm), though of almost bony hardness.

Modes of Dispersal.—There are five main ways in which seeds (or fruits in certain cases) are scattered:—(1) by the wind, (2) by water currents, (3) by explosive dehiscence, (4) by attachment to animals, and (5) by being swallowed by animals.

(1) Dispersal by means of the wind is well illustrated by dandelion-down and thistledown and the like, where the nutlet fruit, containing a seed, is wafted by the wind, often for great distances. The world-wide representation of the groundsel genus, Senecio, is in part associated with the effectiveness of the fruit's parachuting, due to the development of a tuft of hairs (pappus) on the top of the nutlet or cypsela. The fruit of the common Clematis or Traveller's Joy is a nutlet with a feathery plume on its tip, the hoary appearance of the crowded plumes giving origin to another of this favourite plant's many names—Old Man's Beard. When many fruits are simultaneously set free by the breeze, the plumes are often entangled

in long lines, which float away with a beautiful wavy motion, like silver serpents in the air. The dispersal of the linked fruits may be followed for many yards; but gradually the links are broken. Even then, each feathered achene continues to be wafted until it fortuitously sinks to earth and is more or less fortuitously moored. Unfortunately for man, many "weeds" are effectively spread by this parachuting adaptation.

In some cases the parachute takes the form of a light wing-like expansion, as in the maple, and this brings about a whirling oblique movement when the fruit is wrenched off by the wind. By its gyrations the fruit is borne beyond the shaded zone around the parent tree. The frequency of short distance parachuting suggests that it may be as important as a long journey; but perhaps its frequency merely indicates that it is of course more readily attained. It is particularly common in trees, such as maple, ash, and elm. From the ecological point of view it is almost immaterial whether the parachuting apparatus is carried by the *fruit* or by the *seed*; both arrangements are common. Hairs are attached to the seeds of the cotton-plant (Gossypium), but to the fruits of the cotton-grass (Eriophoron); a wing is attached to the seed of the pine, but to the fruit of the sycamore (maple), like our common British tree misnamed "plane", so different in fruiting from the true plane of London avenues.

An unusual mode of dispersal is illustrated by some desert plants which break off from their roots when mature and are driven by the wind along the ground, liberating their seeds as they go. Such are the American Tumbleweeds and Pigweeds, which illustrate in an interesting way how a desiccation natural to the habitat may be turned to an advantage in dispersal. The Glasswort (*Salsola kali*), one of the Goosefoot order, Chenopodiaceæ, but often called the Russian Thistle, shows the same habit of detachment, and has of recent years become a serious agricultural pest in North America. In the Rose of Jericho (*Anastatica hierochuntina*), a Crucifer of the Mediterranean region, the leaves fall off in the dry season, when the seeds are ripening, the branches fold together, and the whole plant breaks off. It is driven about like a light ball by the wind, but the pods remain closed until it reaches moisture or the rains return. Here may be mentioned the fruit of the Porcupine Grass (Stipa), which has a long spirally twisted awn and at its base a sharp spine. The awn is very hygroscopic, untwisting in moisture, coiling again in drought; and these changes enable the fruit to creep on the surface of the ground and to bore into a minute crevice. The beginning of this is seen in some other grasses and in the "stork's bill" of many wild geraniums.

(2) Many truly aquatic plants, such as pond-weeds and water-lilies, have their fruits or seeds normally distributed by currents.

In adaptation to this mode of dispersal there is often a resistant outer coat which prevents the premature entrance of water, and there is often a layer of air-cavities which secure flotation. The Coco-nut can be carried far by oceanic currents, and is widely distributed on inhabited islands in tropical seas; its original home is uncertain, but there is some evidence for the Magdalena Valley in the north of S. America. There has been a tendency to exaggerate the Coco-nut's adaptation to dispersal by water. The hard waxed epicarp keeps the water out; the fibrous mesocarp makes the fruit buoyant; the thick stone or endocarp prevents injury to the seed when the fruit is battered about on the shore; the milk supplies nutriment and fluid enough to keep the washed-up seed sprouting until the root has penetrated below the surface salt into a freshwater layer of soil. It must be admitted, however, that while Coco-nuts are often found among the jetsam of oceanic islands, they are very rarely known to sprout. They are not known to survive unless man looks after them. Perhaps, however, successful sprouting may occur when exceptional tides or storms land them well above the usual high-tide mark. Probably, however, the adaptations are chiefly useful to prevent injury to the delicate seed when the large and heavy fruit falls from the tall tree.

Familiar in greenhouses is a Madagascar aquatic plant Ouvirandra, in which the leaves that float on the surface become ruptured in growth by a multitude of meshes between the veins, and look like skeleton leaves. In reality this effects a great increase in the surface available for gaseous exchange. In *Ouvirandra berneriana* there is a strikingly adaptive mode of dispersal. The fruit bursts explosively and the buoyant seed floats on the surface, where it rapidly germinates. As it gets free from its wrappings, it sinks to the floor of the stream, and is at once ready to effect root-attachment. This unusual sprouting while free floating probably reduces the risk of being washed away or driven on to the land. Many of the mangroves on the tropical shore effect the same by being viviparous; that is to say, the germination is effected while the fruit is still hanging on the parent tree; hence what drops on to the beach is a young plant able to attach itself before it is swept out to sea.

(3) The shrivelling of the carpels composing a dry seed-box, analogous to the withering and fall of the foliage-leaves, allows the seeds to tumble out; and this commonplace dehiscence leads on by gradations to ruptures sometimes sensational in their explosiveness. Everyone is familiar with the little popgun explosions of the broom pods on a sunny autumn day, by which the seeds are catapulted out to a distance of several feet. There is nothing vital in this, for it is entirely due to the unequal shrinkage of dead cells in the wall of the drying pod. But this is not the case when a touch sets free the five valves of the balsam, whose expressive name of "Touch-me-not"

(*Impatiens noli-me-tangere*) refers to its ready explosiveness. At a touch the ripe valves roll up like springs and send the seeds flying; but the force in this case is due to turgid living cells in the walls of the fruit. The extreme case is the Sandbox Tree (*Hura crepitans*), where the drying fruit explodes with a noise like a pistol-shot and shoots the seeds for a few yards. Explosive fruits are not necessarily dry, for the squirting cucumber of the Mediterranean first frees itself by internal osmotic pressure from its stalk, and then forces out the fluid contents and the seeds through the hole thus formed. In connection with parasites we have mentioned the unique Californian mistletoe, which may shoot its seeds for several yards on to an adjacent branch.

(4) Many fruits are covered externally with hooks or roughnesses which cause them to adhere to passing animals, as is well illustrated in burdock, cleavers, medic, hound's-tongue, and cockle-bur. After a time the external passengers fall off, it may be miles from the place where they became entangled. Darwin called attention to a frequent variation of this method, when birds carry seeds in the mud-balls which are formed on their feet or shanks. Let us cite his most famous case, discussed in the *Origin of Species* (1859). "Prof. Newton sent me the leg of a red-legged partridge (*Caccabis rufa*), which had been wounded and could not fly, with a ball of hard earth adhering to it, and weighing six and a half ounces. The earth had been kept for three years, but when broken, watered, and placed under a glass, no less than eighty-two plants sprang from it: these consisted of twelve monocotyledons, including the common oat, and at least one kind of grass, and of seventy dicotyledons, which consisted, judging from the young leaves, of at least three distinct species. With such facts before us, can we doubt that the many birds which are annually blown by gales across great spaces of ocean, and which annually migrate—for instance, the millions of quails across the Mediterranean—must occasionally transport a few seeds embedded in dirt adhering to their feet or beaks?"

The last word suggests the peculiar case of the mistletoe and the missel-thrush referred to in another connection. For while the missel-thrush often succeeds in swallowing the glutinous berry outright, and may void the undigested seed on some distant tree, what we are sure of is that the ordinary planting of the mistletoe occurs when the missel-thrush wipes from its beak a seed enclosed in the viscid pulp which it has failed to swallow.

(5) A somewhat paradoxical way of securing dispersal is to be swallowed by bird or beast, the success depending on the fact that the seed may be ejected from the mouth or the crop, or may be voided from the food-canal before digestion has occurred. In this way the seeds of some of the stone-fruits and many of the berries are scattered. In this connection there may be some advantage in

conspicuously coloured fruits, yet it must be noted that many birds seem to be colour-blind to bluish tints. Moreover many palatable fruits are inconspicuous, though perhaps sometimes more obvious to their animal consumers than to us. In all probability the frugivorous bird's individual experience and association-forming counts for much. Large "stones" are seldom swallowed; small seeds are sometimes digested; yet on the whole it seems justifiable to say that many seeds are scattered by being swallowed by birds and mammals.

Besides the methods of dispersal which we have mentioned there are others of minor importance, but of much interest. Thus some ants in carrying certain fruits to the nest lose them by the way; squirrels forget some of the nuts they have hidden; earthworms plant the seeds of various trees.

For distant dispersal the most important agent is undoubtedly the wind; but in the case of oceanic islands the water-currents are even more important. Fifteen years after the Krakatoan eruption (1883) had killed off all the plants on the island, fifty-three species of seed-plants had established themselves. Of these 60 per cent., chiefly shore forms, were carried by ocean currents; 32 per cent. by the wind; 8 per cent. by animals.

We have illustrated Plant Ecology in reference to sustenance, environment, reproduction, and linkage with other organisms, and our illustrations must suffice, although they are, of course, very far from representing the whole field of inter-relations. They may serve, however, to suggest the general idea that plants are continually moving towards some betterment—towards more food and more light, towards multiplication and mastery. The concept of purposive endeavour, which is suggested by a study of the higher animals, and is consciously verified in man, does not grip in the plant world, but that is not to say that it is irrelevant. We must think of the plant as if it were continually sending out tendrils which feel for support and often find it. Whence it begins afresh. This is the ecological picture!

THE BALANCE OF NATURE

This old-fashioned phrase sums up many interesting facts which show that Animate Nature is well-adjusted to keep agoing, and that smoothly. Living creatures have been sojourning together on the earth and in the waters under the earth for so many hundreds of millions of years that they have become adjusted into a *system*, which has staying power and is not always tumbling to pieces. Their numbers and their claims have attained to some degree of harmony, and though this is often disturbed locally or temporarily, there is an automatic tendency to get back to a viable balance.

On the Scandinavian table-lands there are large numbers of little

rodents called Lemmings—like small editions of Guinea-pigs; and every four years or so there is an over-population crisis. The lemmings, having outrun the means of subsistence—devoured all the vegetation, in fact—go on a march, from which there is no return. Large numbers are found drowned on the shores of the Baltic and the North Sea, and most of the trekkers come to grief in other ways. Yet after a couple of years things are once more very much as they were. The balance has been restored. In some cases in the past similar crises in the history of other animals have proved too serious, and species have been exterminated; but even more striking is the tendency that things have to right themselves.

A Wave of Life.—In his *Naturalist in La Plata*, W. H. Hudson tells of the summer 1872–3 that it was rich in sunshine and showers, blossoms and bees. The season was also very favourable for mice, which devoured the bees, and became so numerous that one could scarcely walk anywhere without treading on them. Cats became wild hunters; dogs ate almost nothing but mice; foxes, weasels, and opossums fared sumptuously; tyrant-birds, Guira cuckoos, and even fowls became mouse-eaters. Countless numbers of storks and short-eared owls came to assist at the general feast. But the winter was one of continued drought; the herbage was consumed or turned to dust and, with the disappearance of their food and cover, the mice ceased to be. The army of enemies, now in retreat, cleared off the residue of mice so thoroughly that "in spring of 1873 it was hard to find a survivor". The wave of life was lost in the sand, and soon things were as though nothing had happened.

Plants and Animals.—Our object in this section is to analyse and illustrate the ecological idea of the Balance of Nature; and we naturally begin with the most fundamental relation, that between green plants and animals. Those who have tried know the difficulty of adjusting the balance of plants and animals in a self-contained aquarium which is not artificially aërated. At one time the plants get the upper hand and may crowd the water so that the animals have no room to move about. At another time the animals get the upper hand, and by devouring all the plants leave a water so poor in oxygen and so abundant in carbon dioxide that they suffocate. In other cases the animals are poisoned by their own nitrogenous waste products, which are normally absorbed and utilised by the green plants. Now, the point is that these aquarium disasters are very unusual in natural conditions.

The most fundamentally important vital process in the world is the photosynthesis effected by green plants. They utilise the energy of the red-orange-yellow rays of the sunlight to build up carbon dioxide and water into sugars and other carbon-compounds, at the same time liberating oxygen as an all-important by-product. The carbon-compounds made in the green leaves form the food of the

plants themselves, and of all the animals that feed on plants. Even when the animal is a thoroughgoing carnivore, a few links in the nutritive chain bring us back to green plants. All flesh is eventually grass and all fish is eventually diatom. The green plant, whether grass or diatom, finds the raw materials of its food in carbon dioxide, water, and dissolved salts; and the synthetised nutritive compounds —carbohydrates, fats, and proteins—are abundant enough to sustain the animal world as well as the plants themselves. Locally and temporarily, as in plagues of voles or of locusts, the animals may devour all the available plants; but it is plain that this is a rare, not a normal, occurrence. On the whole, the nutritive balance is preserved.

Not less important, though less frequently realised, is the fact that green plants have made the oxygen of the air, on which animal life depends. The original atmosphere of the earth was rich in carbon dioxide and water vapour; it had relatively little nitrogen and *very* little oxygen—the production of which has been and continues to be to the credit of green plants.

THE LIVING AND THE DEAD.—Surprise has often been expressed at the fact that we do not usually see many dead animals lying about. After storms the flat beach is sometimes strewn with sponges, zoophytes, jelly-fishes, starfishes, sea-urchins, and molluscs, which are thrown up in profusion by some peculiar combination of wind and wave, but on land it is very rarely that we see any analogue of this jetsam. We have known of two hundred small birds being gathered in one farm-yard after a night of very severe frost, but such an occurrence is so rare in North Temperate countries that we remember it all our life. Part of the reason for the rarity of dead animals is that so many creatures are devoured by others; and another part of the reason is that there are numerous scavenger animals, such as sexton beetles and the larvæ of carrion flies, which bury or do away with the dead bird or mammal. Deeper, however, is the rôle of Bacteria, which are of great assistance in securing the smooth working of Nature. A dead animal rots; that is to say, its tissues are broken down by Bacteria and converted in course of time into salts, ammonia, and water. What is restored to the soil may soon be absorbed by the roots of plants, and even the ammonia that steals off into the air may be recaptured and brought again into the service of life. Thus Bacteria complete a wide circle; they unite dead animal and living plant.

NUTRITIVE CHAINS.—There are many familiar illustrations of what may be called a nutritive balance between different kinds of animals. Thus gulls often eat fishes, and fishes often eat crustaceans, and crustaceans often depend on diatoms; and some sort of balance must be sustained, year in and year out. A correlation has been convincingly worked out between the catch of mackerel, the

abundance of the small crustaceans called Copepods, and the density of the marine population of microscopic Peridinid Infusorians, besides the still more minute Diatoms, which form a very important part of the stock of the sea-soup. If one link in the nutritive chain is weakened, say the Diatom link by lack of sunshine, the result may be felt at Billingsgate.

It is said that a pound of cod's flesh involves the cod's consumption of ten pounds of large whelk or buckie, and that a pound of this muscular Gasteropod demands for its construction ten pounds of sea-worms; and that a pound of worms is in turn the reincarnation of ten pounds of microscopic organisms or organic particles. Thus in eating a pound of cod's steak for dinner the hungry man is devouring a thousand pounds of transmogrified sea-dust; and the world is full of these cycles of reincarnation or re-embodiment. This illustrates the idea of nutritive chains, which contribute essentially to the Balance of Nature.

This large biological idea of nutritive chains finds many illustrations that affect practical interests. Thus it has been noticed in some parts of Britain, e.g. the garden of Moray, that the habits of Herring Gulls have changed very much for the worse during the last generation. They have become less markedly fish-eaters and very hungrily vegetarian. They sit on the "stooks" in the harvest fields and gorge themselves with corn. They work up the rows of turnips, scooping out one after another, and pecking at more than they devour, thus opening the way to fungi and threadworms. How has this change come about? Part of the answer is that Herring Gulls have become much more numerous. This may be because the natural enemies of the young, such as Sea Eagle and Peregrine Falcon, have disappeared or become rare; or because the eggs are not collected so systematically as in former days; or because some measure of protection has been extended to the adult birds. And if it be objected that there are plenty of fish in the sea for all the gulls, the answer is that gulls do not dive and are therefore restricted to fishes swimming near the surface. It is quite possible that around some parts of Britain there are not enough of these to meet the demands of the increased numbers of Herring Gulls. Hence the change of diet.

Plagues of Animals.—The sound Natural History objection to any rapid elimination of any type of animal is that it may result in a disastrous disturbance of a long-established balance. To some extent it is good sense to connect the increased multiplication of voles and the like with the destruction of the natural checks to their increase, such as hawks and owls, weasels and stoats. This is not the whole story, for climatic cycles have their influence; but it is one factor in the mischief. And it cuts both ways, for it has been shown that the supply of fox skins in Hudson Bay Territory

drops when the lemming population is much reduced by starvation or epidemic.

Of great importance in connection with agriculture is the balance between small rodents and small carnivores. An upsetting of this spells disaster, as the rabbits in Australia illustrate tragically. For in the main the prodigious multiplication of those that were imported to the great Island Continent was and is due to the absence of the natural carnivorous checks. The same is true in regard to the calamitous increase of European sparrows in the United States, into which small numbers were imported on repeated occasions, in the hope of countering the attacks of elm-tree caterpillars.

Whether natural checks are exterminated or were never present is immaterial; and the introduction of newcomers into a country without adequate natural checks will have, of course, the same results as the elimination of the natural checks in the old country.

Everyone knows the instructive story of the introduction of the mongoose into Jamaica. There are several kinds of these energetic, fearless carnivores in Africa and India, and they serve a very useful purpose in checking the increase of small rodents and of snakes. To check the imported Oriental rats, which have followed man like a shadow in all his voyages, the mongoose was introduced into Jamaica, where it did good service. It not only counteracted the rats, but it turned its attention effectively to the native "cane-rats", small murine rodents very destructive in the sugar plantations. But having finished with the rodents, the indefatigable carnivores, who had now multiplied considerably, began to attack the poultry and the young of ground-nesting birds. They also attacked certain lizards and snakes, and several species were exterminated. But both the birds and the reptiles had been playing a useful part in checking the multiplication of various injurious insects, which now began to increase, to the great detriment of various crops. Thus the cure began to evolve a new disease, and this particular case is but one out of many. Consequences are not single, but multiple.

Operating on Nature is like playing chess, one has to try to see the distant consequences of a move. Some years ago, in the North of Scotland, a price was put on the squirrel's head, because of the serious damage it was doing in eating off the tops of young forest trees. But as the squirrels' heads came tumbling in, month after month, for two or three years, all with the forester's approbation, a cloud rose in the sky, just as with the mongoose in Jamaica, for there was an alarming increase in the numbers of wood-pigeons. And these birds are on the black-list as far as agricultural interests are concerned. The connection, far from obvious at first, is that

squirrels, vegetarians though they be, are unable to resist the gustatory appeal of the young pigeons they see in the nests on the trees. So the fewer squirrels, the more wood-pigeons, and the worse for the farmer.

Of all these natural checks, the one that means most to man's interests is between insectivorous birds and injurious insects. When we think of the legions of plant-bugs (Rhynchota), the hosts of larvæ, such as caterpillars, leather-jackets, and wireworms, the minute Diptera like the Frit-fly, the phytophagous beetles like cockchafers and weevils, besides sawflies and scale-insects, and the frankly destructive tribe of locusts, we realise that the increase of injurious insects is a continual menace to the kingdom of man, which, after all, depends as yet on the green plants of the field. If the cloud of insects should thicken and spread for a few years, then is all the labour of creation undone. Local plagues, now of locusts and again of caterpillars, here of cotton boll weevils and there of Phylloxera in the vineyard, hint to us loudly that our whole economic system may be readily imperilled if the natural checks to the multiplication of injurious insects should cease. Changeable weather puts an end to many insect-pests; a few commit race-suicide by devouring all the food, but this is rarely possible with field-crops; fortunately for man, insects are often against insects, ladybird beetles against green-flies, and ichneumons against caterpillars, and so on; spiders, frogs, toads, lizards, and other animals do their bit in decimation; but on the whole, what matters most is that there should be an abundance of insectivorous birds, for they form the most important of all checks to the multiplication of injurious insects. We do not ourselves believe that there are data for prophecy, but some naturalists of distinction have said that if our insectivorous birds were wiped out—and they are being continually menaced—our whole bionomic system would come to an end within six to ten years. But whether this is or is not a sound prediction, it is absolutely certain that every reduction in the numbers of those species of birds that feed on injurious insects means a loss to agriculture.

Flowers and their Insect Visitors.—No naturalist can have any antipathy to insects, even when they puncture the farmer's and gardener's and colonist's inflated hopes. They are so intriguing, so subtle, so masterful—with as much right to live, if the phrase has any meaning, as any other kind of creature. They are fascinating, even when they are sinister. Many of them are directly beneficial to man, as silk and honey so well illustrate; others, like ichneumon-flies, are invaluable in checking pests; but the insects that mean most to man are those which secure the cross-pollination of flowers. In search of nectar and pollen, so often advertised by brilliance and colour, by fragrance and form, many

insects, such as bees, butterflies, and two-winged flies, visit flowers and unconsciously secure cross-pollination. Without pollination the possible seeds or ovules cannot in ordinary cases become real seeds that will germinate; and cross-pollination tends to secure, not only more seeds, but a better quality. Thus one of the most important instances of the Balance of Nature is that between flowering plants and their insect visitors. This is not affected by the fact that some of the plants that are most valuable to man, such as cereals, are pollinated by the wind-borne pollen-grains.

We have said enough to illustrate the biological idea of the Balance of Nature, necessarily referred to in other connections in the book. Different kinds of living creatures have evolved together and become mutually dependent, so that increase or decrease on one side of the correlation inevitably affects the other. This is of great practical importance, warning man against upsetting what has been long established and automatically adjusted in Nature. The destruction of insectivorous birds means multiplication of injurious insects; the introduction of rabbits into a new country where their natural enemies are not represented leads to agricultural disaster; the careless introduction of weeds into new surroundings where they are not kept down has often been calamitous; even the apparently irreproachable destruction of poisonous snakes may be soon followed by a plague of small rodents which they helped to keep within bounds. Ignorance is usually very costly, and not least when it disturbs the Balance of Nature.

DETAILED ILLUSTRATION: BIRDS AS POLLINATORS

We have dwelt on the familiar linkage between flowers and their appropriate insect visitors, such as bees and butterflies. On ends of their own, the search for nectar in particular, the insects fly from blossom to blossom and, as Aristotle noticed, they often keep for a time to the same kind of flower. Bees, as Darwin said, are good botanists, and if they visit in succession various members of the same species, they effect cross-fertilisation.

In default of insect visitors there is the possibility of fertilisation by wind-borne pollen, as in the case of pine-trees and many grasses. Or the plant may be able to effect self-fertilisation, as in the case of the common edible pea. There is also the remarkable possibility, illustrated by the dandelion and a few others, that the flower may become parthenogenetic, the egg-cells developing without being fertilised at all. But the likelihood is that if the appropriate insects ceased their visits, many of our familiar wild flowers would disappear from the face of the earth, through

being unable to make any new adjustment for securing adequate fertilisation.

But the question rises whether other visitors besides insects may not effect pollination, and one's thoughts naturally travel to birds, also creatures of the air. It has been known for many years that certain birds acted as pollinators, but a recent investigation by Dr. Otto Porsch has proved that the rôle of birds in this capacity is much greater than has been hitherto realised. He finds that in Java alone sixteen per cent. of the families of flowers have bird-visited species, and that these are pollinated by twenty-two different kinds of birds.

Excluding all those birds that visit flowers in search of insects, as their stomach contents prove, Porsch has evidence of 1,600 different kinds of birds, in thirty-one families, that habitually act as pollinators! They belong to such families as humming-birds, honey-birds, and sun-birds; and what they are in search of is the nectar. These flower-birds are usually small in size and strong on the wing, so that they can land on the flower or poise before it like humming-bird hawk-moths. They tend to have a longish pointed bill and an elongated protrusible tongue, sometimes brushlike, with which they can lick up the nectar. Birds usually require a relatively large supply of water, and this is not always available in the tropics. Hence the advantage of being able to tap the nectaries of flowers.

That the nectar is food as well as drink is obvious, and it often has other valuable components besides sugar. It has been proved that some kinds of flower-birds keep to one particular type of flower, and though they are not concerned with the pollen, they carry it on their forehead from blossom to blossom.

But just as there are special flower-birds, so there are special bird-flowers, belonging to such types as honeysuckles, tropæolums, fuchsias, gardenias, mallows, and irises. They tend to have conspicuous colours, including pure white, and long tubular corollas. They are usually odourless, and will therefore make little appeal to bees, which live very largely in a smell-world. They are particularly characterised by the copiousness and liquidity of their nectar, and some of them have very interesting adaptations that make it difficult for the nectar-receptacles to overflow. There are no bird-flowers in Europe, and part of the explanation is that if a bird is a habitual nectar-feeder it must be able to get supplies throughout the year. In other words, bird-flowers and flower-birds are most likely to be found in places with a perennial flowering season. This does not apply in the same way to insects, which are mostly in an inactive state throughout the winter. In any case, it has been proved, by Porsch and others, that in warm countries an important rôle in pollination is filled by nectar-sipping birds.

ANOTHER ILLUSTRATION: INTER-RELATIONS OF TERMITES

The idea of ecological linkages between organisms may be usefully illustrated by taking one kind of animal and showing how many other vital circles its circle intersects. A very good case is furnished by the Termites or White Ants, forming the order or sub-order Isoptera, not in any way related to the true ants, which are included, along with bees and wasps, in the order Hymenoptera. The social organisation of the termites is discussed in connection with social animals; here it is only necessary to say that a typical termitary contains (1) the so-called "king" and "queen", the functional male and female; (2) and (3) two different kinds of fertile "complementals" or reserves, which may be promoted if some evil befalls the royal pair; (4) and (5), normally sterile workers and soldiers, arrested individuals of both sexes, thus differing from the workers among ants and bees, which are always arrested females.

Most termites live on dead wood or decaying vegetation, and thus they not only assist in the general circulation of matter, but have some rôle as pruners of trees. That they can thrive on dry-as-dust food is explained by the presence of numerous symbiotic Infusorians in the food-canal, for these prepare the minute particles for further utilisation by the insects. Most termites are more or less blind and they are perturbed by the glare of day. They also like a slightly humid and very stagnant atmosphere. These conditions are afforded by the nests or termitaries, which are made of salivated earth or chewed wood or both, and though the constructions are often strong enough to bear a man's weight, they submit to weathering in the course of time, and thus contribute to soil-making. The lucifugous workers make earthen tunnels up the stems and along the branches of the trees, and although these are usually very hard, they break down in the long run, and the component particles may be swept away by the torrential tropical rains to swell the alluvium of a distant valley. Thus, in some measure, termites act as soil-makers, though their rôle in this connection is not nearly so important as that of earthworms.

Although white ants are not related to true ants, there are some remarkable parallelisms in their habits. Thus both of them sometimes cultivate edible fungi, and the termites make intricate labyrinths of masticated wood, on the walls of which the palatable fungi are grown—another instance of wheels within wheels. Various insects, the "termitophiles", habitually live in association with termites, just as other kinds do with ants; and in both cases the associates may be grouped as predatory intruders, actual parasites, tolerated guests, and much-esteemed pets. The last exude secretions

which are greedily licked off by the termites, the pets receiving regurgitated food in exchange. It must be admitted, however, that some of the pets and guests help themselves to young termites—of which there is a plethora. Most of the termitophiles are small beetles, but there are representatives of other orders, such as Diptera.

Very remarkable is the development of a pathological condition called physogastry, among some of the pets. It involves an ugly enlargement of the abdomen, an accumulation of fat, even blindness and winglessness, and it is regarded by Prof. W. M. Wheeler as the direct nemesis of the confinement within narrow galleries and chambers, the very limited supply of oxygen, the absence of light, and the abundance of carbohydrate food. This "physogastry" is one of the few phenomena in Wild Nature approaching an occupational or environmental disease.

Termites are often devoured by other animals, from ants to ant-eaters, the largest enemy being the Aard-Vark, which burgles some of the big African termitaries, whipping in thousands of workers on his long, worm-like gluey tongue. The termite mounds sometimes shelter other animals, such as scorpions, snakes, lizards, and even birds; but very little is known in regard to these associations. Most are probably casual and of short duration, for the termites have irresistible jaws and also the power of emitting a strongly corrosive secretion. Yet R. B. Cowles has found that in Natal the huge monitor lizard, *Varanus niloticus*, habitually lays its eggs in the shelter of a ground termitary. In British Guiana a tree-termitary is similarly utilised by the large Teju lizard.

A quaint detail has to do with a particular caste of soldiers, called nasuti, which are not provided with the usual exaggerated mandibles. They squirt out from their mouth a jet of glue-like secretion which proves very embarrassing to such assailants as true ants. For the inveterate antipathy between white ants and true ants is another of the many linkages. When true ants get a footing in a termitary they are very difficult to dislodge, but they show a strong dislike of the nasuti!

Our point is clear, that if we could imaginatively place one leg of a giant pair of compasses in a termitary and describe a circle on a large scale with the other leg, how many other circles would it intersect—from trees to fungi, from ants to ant-eaters, from Infusorians to beetles, and so on and on. The circle of human life is also intersected, and that in many ways. Everything wooden yields before the appetite of termites, and they do great damage to floors and rafters, to furniture and boxes, to books and papers. In many places wooden telegraph-posts are quite out of the question, and one has heard of situations where it is dangerous for a man with a wooden leg to rest too long! The housewife in tropical and subtropical countries has periodic searchings for the queen termite,

often a conspicuous creature when the abdomen swells from half an inch to four inches, the dilatation being partly due to myriads of eggs and partly to the abundant nourishment which the workers provide. She sometimes lays 30,000 eggs in a day and ten million in a year; and this may go on for ten years. It is therefore very important for household comfort to find the queen—one of the most prolific mothers in the world.

The Australian Bushmen make temporary ovens of the big termitaries, and may even eat some of the salivated clay; the Hillmen of India eat the termites themselves—the queen being regarded as a special delicacy; the pulverised earth of the mounds is often used as a basis for tennis courts and the like. So on and on the linkages run.

OTHER INSTANCES OF INTER-RELATIONS

Inter-relations of the Bracken.—A clear instance of a still unconquered enemy may be found in the bracken—a very serious enemy, though it adds so much beauty to mountains and moorland in Britain. This common fern is so vigorous in its growth that it smothers, and thus kills out, the grass and other pasture-plants on which the hill-sheep depend. Every year it seems to be steadily reducing the pasturage on hill farms. And besides destroying the pasture, it is harmful in other ways. Thus in a recent study Mr. G. F. Scott Elliot points out that sheep, especially tups, forcing their way through the bracken, get cuts on their forehead below the horns, and that flesh-flies attack the wounds. The parasitised sheep may lie hidden by the tall bracken until it dies. The sheep-tick, *Ixodes ricinus*, believed to be the carrier of the disease called "trembling", often finds shelter in the bracken, and the same holds for a fly that troubles cattle and horses, *Hippobosca equina*, whose pupæ are found in the humus at the base of the bracken-shoots.

Reduction of Natural Shelter and its Influence on Wild Fauna.—Gilbert White, who published his evergreen *Natural History of Selborne* in 1789, at the time of the French Revolution, was like Darwin in his appreciation of the linkages or inter-relations between living creatures, and in his vivid sense of the cumulative importance of minutiæ. Both of these qualities are well illustrated by his famous letter on earthworms, whose importance as soil-makers and soil-improvers he clearly recognised. But this was characteristic of Gilbert White's outlook—he had the vision of *the web of life*. In the heat of the day the Hampshire cattle stand in the forest ponds, and their dung, dropped into the water, forms a culture-ground for aquatic insects—a very welcome addition to the food-supply of fishes in places where "the water is hungry and the

bottoms are a naked sand". He quaintly adds: "Thus Nature, who is a great economist, converts the recreation of one animal to the support of another." How interested Gilbert White would have been in the modern disclosure of the part that Japanese cattle, standing in the water, play in the spread of the formidable human parasite called Bilharzia—but that is certainly another story.

Nothing lives or dies to itself. The naturalist of Selborne noted that troops of water-wagtails run about the cows that are feeding in moist low pastures, and pick up the flies attracted to the cattle, or the other insects disturbed by their hoofs. How interested he would have been in the now familiar fact that these water-wagtails check the spread of liver-rot in sheep, since they are particularly fond of the little water-snail (*Limnæus truncatulus*), which is the host of the larval stages of the liver-fluke that causes the sometimes serious "rot".

Further illustrating this central ecological idea of inter-relations, let us notice some of the results that follow the reduction of wild corners throughout the country. From the farmer's point of view there is, no doubt, much to be said for trimming hedgerows and doing away with weedy borders and wild corners in fields, for these are often the haunts and nurseries of insects injurious to crops. Nevertheless, the other side of the account must not be overlooked, that hedgerows and the like afford shelter or cover to birds and other creatures, many of which are conspicuously or inconspicuously the farmer's friends. The more garden-like a countryside becomes, the greater is the risk that useful components of the fauna will disappear for lack of shelter. Tidiness may easily be carried too far!

THE CHANGES GOING ON.—Both Gilbert White and Charles Darwin realised, as we have said, the cumulative importance of little things; and this must be kept in mind in connection with changes in the countryside going on to-day. A particular reduction of shelter or cover may seem quite trivial, but the sum-total of results, over a large area and for a long stretch of years, may be of far-reaching importance. Another preliminary caution is that there are few changes which are one-sided in their results; most are partly against and partly for human interests. We have no warrant for expecting that Nature—"friendly" as she often is—should always operate in man's favour. Thus, while there are a few birds, like wood-pigeons, that are almost wholly on the minus side as far as agriculture is concerned, and while the great majority are almost altogether to the good, of not a few it must be said that if they do some harm, they also do much good. There are familiar and long-standing arguments, pro and con, in regard to such birds as rooks, such mammals as moles, such insects as wasps. In many cases, like the last-mentioned, the data are not yet abundant and

precise enough to warrant us in saying to which side—for or against agricultural interests—the balance swings.

It is also to be noted that the spread of agriculture is in itself bound to have a nemesis by promoting artificial situations. The Colorado Beetle was of no great moment as long as it fed in Colorado on its original food-plant, the Sand Bur Solanum, but when fields of potato (another Solanum) afforded abundance of appropriate food, and when field was joined to field across the United States, then there was a plague—still unconquered.

Reduction of Shelter.—The reduction of shelter includes (*a*) the extension of farm-lands over corners which had long retained their natural wildness, such as furze-covered commons where birds like Yellow Buntings used to breed, or slopes where the Badger or Brock used to burrow (how many local names begin with Brock!); (*b*) the stripping and restriction of the old-fashioned big hedges, which used to shelter useful mammals like Hedgehogs and useful birds like Hedge-sparrows; (*c*) the replacement of hedges by wire fences and stone walls; (*d*) the making of broad roads, at present so frequent, and in some cases necessary, the first stage being usually the removal of the often luxuriant strips on either side, and the substitution of covered-in drains for the old-fashioned ditches, in or about which many creatures had their homes.

We must repeat that the ranks of the injurious are thinned as well as those of the beneficial; but there can be no hesitation in saying that, from the agriculturist's point of view, there is much to be said for such mammals as hedgehog, weasel, and shrews, and for such birds as thrush and blackbird, titmice and wheatear, robin and cuckoo. Scores might be added which are more or less thirled to hedgerows and wild corners. Slow-worms, which are almost restricted to wild places, feed largely on slugs; lizards are mainly insectivorous; frogs and toads are all to the good; and all these are dependent for continuance on the persistence of appropriate wild shelter.

Old and New.—In old days the cutting down of forests meant the disappearance of many animals, such as the Woodland Reindeer and the Elk, the Beaver and the Bear, the Wolf and the Lynx; and our present point is that the dwindling of copses, hedgerows, and wild strips, which are the "forests" for many small creatures, is being followed—and that inevitably—by a reduction in our fauna.

It is true, no doubt, that the wild fauna of Britain has not, as a matter of fact, diminished *quantitatively* in modern times; but it has lost in *quality*. There has been a replacement of larger by smaller forms of life, and of the visible by the invisible. As Ritchie proves so convincingly in his great book, *The Influence of Man on the Animal Life of Scotland* (Cambridge, 1920), man "lops off the giants at the head of the scale, and adds pigmies at the bottom—insect marauders which enter unobserved and are often first noticed

only when they force themselves upon his attention in their myriads". To gain rabbits and rats, cockroaches and bugs, is no consolation for losing reindeer and elk, beaver and pine-marten, bustard and crane. Of course, no one dreams of proposing to reinstate bears and wolves (fox-farms and the like being an entirely different proposition); but no one can doubt the agricultural danger involved in over-thinning the ranks of insectivorous birds and of small carnivores that check the multiplication of small rodents.

To continue to argue from the past to the present, the necessary spread of cultivation and the breaking in of waste land long ago involved many disappearances, like that of the Great Bustard (*Otis tarda*)—once as common as a wolf and now as conspicuous by its absence—or that of the quail (*Coturnix coturnix*), once as common as now it is rare. It nests occasionally in Scotland, but more frequently in Shetland, where the "reaper" is still unknown. "There, after the manner of the old days, the scythe or the sickle still mows the waving corn, and the quail reaps the benefit of such peace as a primitive cultivation gives." The immediate point is whether what happened to the Bustard and the Quail is not now happening to the Corncrake and, perhaps, also to the Lapwing, best of "farmer's friends". It is not merely that these birds do not approve of reaping-machines: there is a reduction of rough corners beside fields and of quiet places generally. Even when the hedge has gone, the partridge often finds a suitable nesting-place in the rough growth beside a road-side wall, and on the outer side as well as on the inner! But even these residual strips are being reduced, and in proportion as things become "spick and span" the birds become scarcer.

We do not counsel the impracticable, for cultivation must needs become more extensive and more intensive; but it is a practical question whether there might not be more conservation of wild corners as sanctuaries for beneficial animals. Yet again, in all these balancings of pro and con we must be jealously fair, and while there has been in some highly cultivated parts of the country a diminution of the finer butterflies, for instance, that used to be common—and this as the result of the elimination of the caterpillar's food-plants from hedges and fallow strips—the same will be true in regard to many *injurious* insects. So the reduction of wild shelters cuts both ways.

But this all-round fairness is a little apt to lead us to be too optimistic; the ominous fact is that there has been a serious reduction of the native shelters for useful birds and beasts. Dr. Ritchie puts it well: "With the breaking in of the wild banks and braes—'the burnin' yellow's awa' that was aince alowe, on the braes o' whin'—the nesting-sites for many small birds and the shelters for many small rodents and insectivores have disappeared, to the

grievous reduction of their kinds." We have deliberately cited this reference to rodents as well as insectivores, though the rodents are the farmer's foes while the insectivores are his friends. Nature is very fair-minded; she is not prejudiced in favour of farmers.

Drainage Plus and Minus.—Another useful analogy may be found in the results of drainage, ancient and modern. In old times there were enormous tracts of Britain in the state of peat-bogs and fens. Curlew and bittern, waterhens and snipe used to be at home in what is now Belgravia, and the same may be said of many a prosperous farm. As drainage became common and effective, vast swamps were reclaimed for agriculture; and Britain lost its cranes and bitterns—the latter now happily returning to breed in the Norfolk Broads. This drainage had, of course, its plus side, for thousands of acres of swamp became farm-land, and as drainage meant a reduction of pools suitable for mosquito larvæ and fresh-water snails, there was a diminution of malaria or ague, once very common in Britain, and of liver-rot in sheep, still abundant in places where effective drainage is difficult. What happened in the past on a large scale is now happening in many places on a small scale. There is a reduction of ponds and pools, bogs and ditches, and while this has its agricultural and sanitary value, there is no use trying to ignore the tax to pay.

Even on golf courses, which have their ecological aspect as reservations for wild life, there is a persistent tendency to reduce the "rough" and to dry up "the pleasant places of the wilderness"—all with the result that many wild flowers, which once were common, have now vanished, and that many birds, whose presence used to console the bad golfer, have said farewell. The inevitable nemesis comes, even to the well-entrenched golf club, when there are not birds enough to check the multiplication of Daddy-longlegs and Click-beetles, whose larvæ, the "leather-jackets" and wire-worms, are so hostile to the turf. So far as we know, it serves little purpose to allow a pond-surrounding swampy nesting-ground of Black-headed Gulls to become so dry that the birds abandon it; for one of the immediate results is that the adjacent fields, formerly so free from insect pests, thanks to the appetite of this useful species of gull, are no longer exempted. We do not pretend that this has been proved by a careful statistical correlation of the amount of swampy ground and water-surface, the number of gulls in the gullery, and the abundance of injurious insects in the surrounding fields—inquiries that take time and have also to be corrected in relation to weather, farming, and crops—but the observational impression is as we have stated.

Dr. Ritchie gives details of a very instructive history of Black-headed Gulls. They came (1) in 1892 or 1893 to a heather-moss, with peat and moisture underneath, on the southern slopes of the

Pentland Hills; (2) they were protected and encouraged by the proprietor, who fed his young pheasants on the gulls' eggs; (3) they nevertheless flourished, the last clutch being always left to hatch; and (4) they increased enormously till (1897) there were 1,500–2,000 pairs of birds. The grouse that used to frequent the heather disappeared. But with the extension of the gullery the vegetation (5) underwent a noticeable change, the heather being replaced by abundant coarse grass, which was cut for hay, then by a dense growth of rushes, both (6) becoming almost choked by a forest of docks. Whereupon the villagers, angry at the destruction of their hay-crop, made persistent raids on the gullery, and the proprietor, regretful at the disappearance of grouse, ceased to protect the gulls for his pheasants. In 1917 not more than thirty pairs nested, where a few years before there had been some two thousand pairs. Then the vegetation began to change back again (7), the docks and rushes giving way to rough grass and even to heather. Finally, the grouse began to return!

Roads and Horses.—We have referred to the trimming and broadening of roads, with the resulting decrease of shelter, but there are two other points to be considered. The modern road adapted to motor-traffic has in many cases something in the way of tar-macadam or asphalting; and it is generally believed that the wash after rain is detrimental to the small animals in ditches and streamlets, and directly or indirectly to trout and salmon in the adjacent rivers. This may possibly mean the destruction of the young stages of some injurious insects, but it also implies a reduction of part of the food-supply of insectivorous birds. It may be replied, however, that this will be far more than outweighed by the augmentation of insects implied in the increase of farm-land with its abundance of suitable food-plants. The issues are so manifold and criss-cross that it is next to impossible to predict the final result of more or less necessary changes; but the general proposition is this, that extensive crops afford superabundant food to insect-pests—such as turnip green-fly, turnip moth, turnip saw-fly, turnip flea-beetle and diamond-backed moth; that a promiseful counteractive of these plagues is the multiplication of the birds which prey upon them; and that this implies a conservation of suitable shelter and cover.

The numbers of field-insects must be incalculably greater than in old days, when agricultural operations were less extensive; and that ought automatically to mean more birds. Yet it may sometimes mean a disproportionate increase of certain types of bird, such as starlings, which are apt to drive away smaller insect-eaters, like wrens, robins, and warblers, which, moreover, are more dependent on the minor shelters like hedgerows, the starlings mostly roosting in trees.

Some birds, that are largely seed-eaters, like the finches, may be beneficial to agriculture, inasmuch as they feed their young on

insects. Thus the common Yellow Bunting or Yellow-hammer, which depends on seeds and small fruits in winter, is largely insectivorous in summer, and feeds its young on insects. The fact that it, like the Hedge-sparrow, is also fond of spiders, may be noted as an instance of the difficulty of balancing pros and cons, for spiders are very useful in checking the multiplication of small insects.

In many parts of the country where the Yellow-hammer used to be very common, there is now a marked scarcity. This is ascribed by some to the fact that there is of recent years so little horse-dung on the roads; it used to be a common sight to see the Yellow-hammers picking up the undigested grains of oats.

In Conclusion, it is quite certain that the food of many wild birds consists largely of injurious insects which are a continual menace and involve a huge annual loss which no country can afford. Thus there might be mentioned from the long list the following representative birds: titmice, lapwings, hedge-sparrows, redbreasts, skylarks, thrushes, wagtails, warblers, pipits, and flycatchers. These and scores of other birds are worthy of preservation on grounds of utility—let alone higher values—and one way of securing their survival is to refrain from being over-zealous in doing away with more or less harmless shelters.

THE INTRICACY OF LIFE.—From the illustrations given it is plain that the old-fashioned Natural History, which needs no apology when we think of masters like Réaumur and Gilbert White, is being replaced by the modern sub-science of Ecology, which expresses the same ambition to understand living creatures in the plural and in relation to their surroundings, both animate and inanimate. It is what Semper called "the higher physiology", the study of life as it is lived in Nature, where the circle of each individual's interests is intersected by many other circles—such as kindred, members of the same species, neighbours, competitors, deadly enemies, parasites, symbions, and so forth. To Pearse and to Elton we owe two good English-written books on *Animal Ecology*, and everyone knows Tansley's *Plant Ecology*. All we wish to do here is to emphasise the general impression—the intricacy of life's inter-relations.

One of the main tasks of ecology is to decipher the patterns in the web of life, and as the inquiry is being pursued with precision and penetration it is becoming plain that the intertwining of the vital threads is even more intricate than was supposed by the old-fashioned Natural History with all its scrutinising insight. Darwin was a modern ecologist in his appreciation of the work of earthworms, so much deeper and more convincing than Gilbert White's anticipations.

For centuries there has been admiration of the parental care exhibited by many insects, but who ever suspected the extraordinary nutritive exchange or "trophallaxis" between some mother-wasps or worker-wasps and the grubs in their cells? In many cases the mothers or stepmothers feed the grubs with the chewed flesh of insects, the jaw-apparatus of the larvæ being very poorly developed. But when the meal is supplied, and sometimes in defect of it, the larva exudes from its mouth a drop of sweet elixir, which is greedily licked off. In some instances the drones have learned the trick, but they give nothing in exchange. This kind of intricacy is being increasingly revealed. It is not that Nature is more of a tangle than we thought, it is rather that the pattern of her fabric is more intricate than it seemed at first.

For a long time naturalists have been familiar with the dry-as-dust meals of the wood-eating termites or white ants, and some have expressed themselves puzzled by the way these insects thrive on such physiologically unpromising material. But who suspected that the termites can make nothing of their food unless there is in their alimentary system a vigorous culture of beautiful Infusorians, found nowhere else, which do something to the food which makes it available and profitable to the termites? And strange facts emerge when we inquire how the soldiers thrive, whose jaws are so big that they are not suitable for chewing wood. But we have already referred to this.

The diagram that ecology has imprinted on our intelligence is that of a circle intersecting and being intersected by many other circles. Thus the hollow petioles of a South American tree called Tachygalia afford shelter to small beetles, which have established an alimentary partnership with minute mealy-bugs. The two insects live together, and the mealy-bugs, which feed on the tissue inside the petiole, yield a supply of honey-dew when the beetles massage them, as they do somewhat forcibly. Tree, beetle, bug—a triple alliance; and when certain aggressive ants appear on the scene, each of these circles is intersected.

Ants and Aphids.—In further illustration of the intricacy of inter-relations in the web of life we take a few deliberately very diverse illustrations—half a dozen out of hundreds. It has long been known that "honey-dew"—the sugary overflow of the aphids or green-flies which feed on plant juices—is a food greatly prized by many insects, and by ants in particular. Many ants have learnt how to stroke the aphids so that a drop of the syrupy fluid exudes. Some ants do this only when an opportunity occurs; but others have come to depend on this "honey-dew" as one of their principal sources of food. Such ants, as we may read for example in Forel's great book (*The Social World of the Ants*), tend the aphids as carefully as man tends his domestic animals: they

keep them, in the cold weather, in their own underground nests; they guard them; they help in the rearing of each brood.

A case of this sort has recently been examined by Eidmann. He describes how, when the buds open in spring, the guardian ants lead the aphids from the nest and on to suitable trees or bushes. There the ants, of which there is one for each individual aphis, or at least for each small group, mount guard over their "cows", as Linnaeus called them, keeping all strangers at a distance. From time to time the ant "milks" the aphis and collects the fluid, either to bring it to the nest or to pass it on to another ant for this purpose. If the night turns cold the ant shepherds the aphis back to the nest; but later in the summer, in warmer weather, the ants retire alone, leaving their aphids on the plants all night. In the morning the ants return and mount guard once more, and by careful marking Eidmann was able to show that it was always the same ant that returned to one aphis kept under observation. If the ant was taken away another soon took its place.

As the summer grows in strength, and the prolific aphids become more numerous, the traffic between the ants' nest and the plants, the "pastures", becomes greater. Underground tunnels are constructed, or at least covered run-ways, extending even up the trunks of the trees. These protected routes are only used during the day; at night, although the traffic is greater, they are not needed and are deserted.

Eidmann took a census of an average-sized nest of the Black Ant he studied, *Lasius niger*. He found in it nearly 3,500 adult worker ants, and three times that number of larvæ and pupæ, most of them destined to become in due course workers. He estimated that in the course of a summer such a colony would consume about a quart of "honey-dew". The aphids thrive so well in the care of the ants that the association may be very harmful to the plants on whose juices the aphids feed.

FILTERABLE VIRUSES.—This is a general name for extremely minute disease-causing microbes which can pass through a fine porcelain filter, and without losing any of their virulence. The first to be recognised (by Iwanowski in 1892) was the one that causes "mosaic disease" in the tobacco plant. It was shown that a healthy plant could be inoculated with filtered juice from diseased leaves, and that the juice retained its power of infection for many months—this clearly pointing to, if not proving, the presence of a living microbe.

But it was not till six years afterwards that the importance of the new idea was recognised. In 1898 Loeffler and Frosch showed that fluid taken from the blisters of cattle suffering from foot-

and-mouth disease was capable of producing the characteristic symptoms in another animal after it had been passed through a really fine filter which kept back ordinary bacteria.

The idea spread that the presence of a filterable virus might afford an explanation of many familiar infectious or contagious diseases in which it had been found impossible microscopically to detect any microbe. At present under this heading there must be at least half a hundred diseases, and as instances we may mention measles and scarlatina in man, rabies in dogs, pleuro-pneumonia and rinderpest in cattle, chicken plague and silkworm jaundice, and various "mosaic diseases" in plants, as in tomatoes, beans, and sugar corn. It is probable that these filterable viruses do not form a homogeneous group, but have some of the physiological diversity of the bacteria themselves. Thus it is probable that some of the viruses contain an enzyme (or ferment) which does deadly dissolving work, and continues doing so as long as it has suitable material to work on; and this would not be inconsistent with the generally accepted view that the filterable viruses are infinitesimally minute living organisms, comparable in virulence to some of the disease-bacteria and disease-Protozoa, but smaller and probably simpler even than the former.

The question rises, however, why it has been concluded that these deadly viruses are or contain organisms at all. Why might they not be non-living enzymes, why not simply poisons? The answer is firstly, that there are no facts known that would suggest the passage of a ferment from one organism to another, either infectiously through water, food, or air, or contagiously by actual contact. No doubt the diffusion of some of the filterable-virus diseases remains obscure, as in the lamentable case of the foot-and-mouth plague, where secure facts are still few and far between. But there are other cases less obscure where the *analogy* is certainly with what occurs in indisputable microbic diseases.

Secondly, in some viruses, such as that associated with chicken plague, the use of devices like centrifuging and the ultra-microscope has been rewarded by the detection of more or less distinctive corpuscles. In the case mentioned they have been measured and found to be smaller than man's red blood corpuscles. Thirdly, we have to keep in mind the analogy of certain well-known diseases where the infective agent is very uncertain, yet the progress of the malady is associated with the appearance of distinctive corpuscles in the tissues. Some authorities would give, as examples of this state of affairs, the human diseases of smallpox, hydrophobia, and sudden infantile paralysis (epidemic poliomyelitis). It is quite possible that the microbes of several diseases may pass through an "ultra-microscopic" phase.

Lastly there are cases where the use of an "ultra-filter" robs

the fluid of its virulence, which supports the view that this depends on the presence of micro-organisms.

Returning for a moment to foot-and-mouth disease in cattle, which has cost Britain alone many millions of pounds in a single year (1923–1924), we should notice that several investigators have claimed success in removing it from the list of filterable viruses. In other words, some believe that the micro-organism has been discovered. Thus, to take a well-documented claim (1924), Profs. Frosch and Dahmen, of the Veterinary College in Berlin, report having detected and photographed the microbe (or its halo) by means of the ultra-microscope. They describe it as an exceedingly minute bacillus, not very far from the diphtheria bacillus. A culture has been prepared which produced characteristic blisters in guinea-pigs and partial attacks have been produced in cattle by inoculation. Dahmen speaks of having attenuated the virulence of the virus, and everyone wishes him success in finding a serum which will render cattle immune to attack. We have lingered over this particular case because it illustrates the tenacious persistence and the progress of scientific inquiry even when the problem is peculiarly difficult, as is the case with foot-and-mouth disease.

In the spreading of "mosaic disease", so-called from the pattern shown by the infected leaf, certain sap-sucking and leaf-eating insects are known to effect the transference from plant to plant. A good illustration of wheels within wheels is afforded by the fact that insects themselves fall victim to the disease. Thus the wilt diseases of the caterpillars of the Nun Moth and the Gypsy Moth are due to filterable viruses, and these two cases are interesting because the results are in man's favour, not against him. The Gypsy Moth caterpillar was accidentally introduced into America in 1869, and has done terrible damage in defoliating trees. The experts seem to think that the appearance of wilt disease has done more towards the eradication of the pest than all man's efforts at control, ingenious and energetic as these have been. Yet what a choice of evils!

THE LIVING EARTH.—We owe to Pasteur the first vivid realisation of the numbers of bacteria in the soil, but long before that there was some recognition of the "underworld" fauna. Thus Gilbert White (about 1777) recognised very clearly that the number of earthworms was very large, and that the work they have done and do is of far-reaching importance. Gilbert White's picture was repainted by Darwin in his well-known masterpiece. Yet we venture to say that one of the gains of twentieth-century ecology has been a realisation of the literal accuracy of the phrase "the Living Earth". There is, for instance, an invisible army of soil-Protozoa that we are only beginning to know; and we are far from having an adequate knowledge of the numerous and diverse insect larvæ

that live in the soil. Similarly our knowledge of soil nematodes is still very fragmentary. Some recent researches by Dr. David Robertson show clearly that there are many different species and that the number of individuals is often huge.

Taking the second point first, we notice that, as an average of ten samples, Robertson found in a cubic inch of soil 65 nematodes from oat stubble, 70 from two years' pasture land, 105 from one year's grass, 115 from a clayey oat field. Of course that means billions to the acre, for even the 55 nematodes per cubic inch of potato land means two billions per acre six inches deep; and the low census of 35 per cubic inch of clayey turnip land means far over a billion per acre. There can be no doubt that the nematode or threadworm population is enormous. It would be interesting to have records from wild soil of various kinds. We know that there are multitudinous individuals of *Tylenchus hordei* (if this species-name still survives), boring into the roots of the sand-binding grass (Elymus) at the exposed shore immediately to the north of Aberdeen. This nematode makes galls on the thread-like roots; and the larvæ can survive, as we have verified, for a couple of years the dryness of a shelf above steam-heating pipes. After two years of this drought they moved about soon after the galls, soaked in water, were teased out.

The second point is the diversity of species, for Robertson found eleven different kinds of *Dorylaimus*, two of *Aphelenchus*, two of *Mononchus*, three of *Rhabditis*, one of *Cephalobus* (the viviparous *C. filiformis*), and two of *Tylenchus*. The disease of "Cauliflower" in strawberry plants is due to *Aphelenchus fragariæ*, and *A. olesistus* does much damage to many plants. "Tulip-root" in oats is due to *Tylenchus dipsaci* and "ear-cockles" in wheat to *T. tritici*. It should be noted that many of the soil nematodes are strictly saprophytic, that is to say, they feed on rotten organic matter. Only a minority are known as parasites in plants. One species may devour another; thus Steiner and Heinly observed that an individual *Mononchus papillatus* devoured 83 larvæ of *Heterodera radicicola* in twelve weeks. Ecology is very intricate.

Returning to soil bacteria, important agricultural developments seem approaching. It is now a comparatively old story that under certain conditions, of intensive culture especially, soil may be greatly improved after heating to a temperature sufficient to kill out undesirable germs, and other plant-enemies as well. But while the farmer has increasingly been applying costly manures of various kinds, and this with the approval and even urge of his scientific advisers—witness the potash-salts of the Alsatian mines, or the nitrates prepared from the nitrogen of the air—some of these experts now begin increasingly to doubt whether so much of such manuring be really the best course after all. For they are finding reasons to

fear that the varied acidity or alkalinity of such manures may be —in many cases, as notably in Mediterranean France, but if so probably elsewhere also—acting prejudicially on the desirable soil bacteria; and they are now consequently beginning to experiment towards the encouragement of these, with hopes of substantial manure-economy accordingly.

THE BEE DANCE.—When an exploring bee discovers some flowers with abundant nectar, it takes in as much as it can hold and makes for home. In a short time there are more bees on the scene. How do they know that there is treasure-trove and how do they find it? As already noted, the experiments of Frisch have thrown light on this. When a bee that has sucked to the full returns to the hive, it indulges in a peculiar "round dance" on the comb. This excites the workers in the immediate vicinity and they hurry forth to find some nectar for themselves. But before issuing from the hive they nose at the discoverer, and thus get an olfactory clue to the kind of flower to be sought after. The discoverer does not fly with them, that is certain. They explore for themselves. But they have got the scent as a clue.

But what if the nectariferous flower has no scent? Frisch's answer is that a hive-bee, excited by a discovery, sprays the blossom with a characteristic scent formed in a protrusible glandular pocket near the hind end of her body. This scent serves as a tell-tale clue to the searching bees.

It has been noticed that when a profitable patch of flowers begins to be exhausted, the visits of "new bees" begin to drop off. In a short time they stop. How is this regulated? The answer is that when a bee returns with little nectar she does not dance; and thus no more searchers go forth. When the bees are collecting pollen, not nectar, there is the same sort of "dance language", but the nature of the dance is different!

HONEY.—In connection with animal industry on the one hand, and the evolutionary importance of nutrition on the other, we wish to take the concrete case of the honey of bees. Honey is transformed nectar that has passed into and out of part of the food-canal of the bee; and nectar is an overflow of the sugar that plants make in their everyday photosynthesis. It sometimes exudes away from the flower altogether in *extrafloral nectaries*, but *floral nectaries* are naturally more frequent, for they attract the insect visitors to come to the right place, that is to say to the flower, where cross-pollination may be effected. When the pollination has come about, then the nectaries close, and the surplus sugar can be diverted into the swelling fruit. If the fruit is dry and not sweet, the surplus sugar can be stored as starch in the seeds or remain as a reserve

in the stem. But the first point to be quite clear about is that the nectar, which was part of the plant's wealth-stores of reserve energy, becomes the chief part of the bee's wealth.

Nectar consists for the most part of cane-sugar, and in the bee's honey-sac, a globular part of the food-canal between the gullet and the stomach, this is changed by the ferment of the salivary juice into two simpler sugars, glucose or grape-sugar and fructose. But the honey which is passed out again through the bee's mouth into a cell of the honeycomb is much more than sugar. In fact, it is a rather complicated mixture. It contains an unchanged residue of cane-sugar, a little mucilage and more than a little water, some wax and essential oils, a trace of pigment and salts, besides grains of pollen which contain protein material. So honey is much more than sugar; it is a delicate mixture of foodstuffs; and many people believe that it prolongs youth and staves off ageing.

The best honey is "virgin honey", made by bees that have not swarmed. It is stored in pure-white cells of translucent wax. Later on in the life of the hive the honey may have to be stored in cells that have been used as cradles for grubs, and these have darker and thicker walls. It is delicious honey still, but not quite so fine, and the older comb is not so inviting. The minor differences disappear when the honey is removed from the comb by the old-fashioned process of "dripping" or by the modern use of a "centrifugal extractor", which whirls the comb round at a great rate. Experts say that this "extracted" and pooled honey is best of all; but the honey from the honeycomb is more interesting to eat, and one cannot help suspecting that there may be a loss of some subtle by-product when the honey is removed from its natural cups. Honey made from artificial sugar given to the bees should not be ranked with true honey gathered from the flowers.

From the Natural History point of view, honey has three aspects. In the first place, along with pollen, it is the bee's food. Some of it passes through a complex combination of valve and sieve into the digestive stomach, and it is said that if solid particles such as pollen-grains get through the sieve, they cannot be passed out again when the bee empties its honey into a cell of the comb. In the second place, along with pollen, it is part of the food given to the grubs after they have been reared for a while on more digestible milky material, which seems to be mainly a secretion from the food-canal of the worker. It may be noted here that not a few insects feed their young by forcing out (regurgitating) food from their food-canal, just as pigeons do in feeding their squabs. In the third place, the honey, with all that in it is, forms a store for the winter—a store that man utilises. It is this storing of honey that accounts for the persistence of the beehive from year to year, in contrast, for instance, to a wasp-community, in which only the

young queens survive the winter. In natural conditions some of the stored honey in the hive goes to meet everyday demands before winter comes, but there is a large surplus that makes a permanent wintering community possible. The honey in the honeycomb is perhaps the most beautiful form of *wealth* in the world—it means stored energy, bottled sunshine. The hive illustrates the value of capital as well as labour.

The sheets of honeycomb hang vertically in the hive, and the hexagonal cells are arranged on the two sides, with their bases towards one another. They are not quite horizontal, but tipped a little upwards, so that the viscous honey does not so readily stream out. But there is another reason for the retention of the honey—it becomes gradually thicker by the evaporation of water-vapour. Thus nectar with 60 per cent. of water may become honey with 20 per cent. Of course some nectars, like that of the Fuchsia, are very dense to start with. An interesting point in regard to the ripening of honey in the comb, where the changing of cane-sugar into grape-sugar continues, is that it is helped by the ventilation of the hive. Some of the bees fan with their wings, and this serves not only to keep the hive from getting stuffy, but also to drive away water-vapour and thus ripen the honey in the honeycomb.

Bees are not the only creatures that appreciate the nectar of flowers. Some of the ants become animated honeypots, hanging, when they are full, from the roof of their house like bunches of yellow grapes! Some birds, like the hummers and the honey-birds, are very fond of the more fluid kinds of nectar; and an occasional sweet-toothed wasp may point the way that the bees followed when they ceased to be carnivorous and became predominantly honey-eaters. For it seems practically certain that bees evolved from a primitive wasp stock. This was a notable parting of the ways, when the bees became refinedly vegetarian and the wasps remained predominantly carnivorous. Notable, because flesh does not store!

FAUNA OF PITCHER-PLANTS.—Prof. R. W. Hegner has investigated the animals that live inside the Sarracenia pitcher-plant of Maine. In the ten pitchers examined there were Protozoa, representing the three chief groups—Rhizopods, Infusorians, and Sporozoa. It is probable that most of these Protozoa are species carried in by the flies which pay fatal visits to the pitchers. It is possible, however, that some of the Protozoa are at home in the strange environment, and it was found that several Infusorians like Paramecium could thrive and multiply when placed in the fluid which the pitchers contain. In addition to the Protozoa there was an abundant representation of insect larvæ, mites, and rotifers. In a few cases there were minute water-fleas and some threadworms.

In one case there was a Tardigrade, or Sloth-Animalcule. The interest of the study is twofold, for it shows how animals may adapt themselves to a very strange and somewhat risky habitat, and it illustrates the characteristic insurgence of animals in seeking out niches of opportunity.

WHALES AND THE LEAGUE OF NATIONS.—There seems to be a growing recognition of man's trusteeship of the Animal Kingdom. For while there is still much to deplore in the way of thoughtlessness and ruthlessness, there seems reason to believe that more and more people are beginning to feel the disgracefulness of allowing the greedy extermination of animals that are not directly inimical.

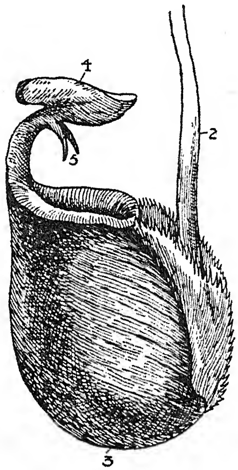


FIG. 40.

Pitcher of a Pitcher-plant (*Nepenthes bicalcarata*), so-called from two peculiar spinous processes (5) below the lid (4). These may help to thwart insect-eating intruders. The main cavity of the pitcher is marked (3), and its stalk (2).

And it is not merely a scientific and æsthetic loss that is involved when a fine type disappears for ever: it may imply a short-sighted economic impoverishment. This applies, for instance, to the whales of the southern seas, which are disappearing rapidly before unregulated fishing. Besides the southern Right whale, Balæna australis, a near relative of the Greenland Right whale, Balæna mysticetus, which used to be so common in the North, there are "finners", "humpbacks", "thrashers", and "blackfish". In the 'nineties of last century these great whales were represented by immense schools in Antarctic Seas, but they have been hunted so persistently of recent years by Argentine, Chilian, Norwegian, French, and British whalers that extinction seems to be already near. This would be an impoverishment of the world's resources,

but it is inevitable if the numerous companies from different countries continue to fish in an unregulated way without any respect to the rapidly dwindling numbers. Therefore, it is good news that a committee of experts has been appointed by the League of Nations to inquire into the possible saving of the southern whales.

The British-American agreement as to northern seal fisheries, made a good many years ago by the respective Governments, after competent zoologists (Prof. D'Arcy Thompson and Prof. Starr Jordan) had been sent out by each to settle matters from the biological, instead of the nationalistic, point of view, affords a good example of the way in which this yet larger question may be settled to the benefit of all concerned.

CHAPTER III

PHYSIOLOGICAL

ANIMAL LOCOMOTION.—It is very characteristic of animals that they can mostly move about in search of food, foothold, and mates, or away from enemies and influences that are hurtful; and this locomotion is effected in a great variety of ways. Among multicellular animals there are four chief methods, which, following F. W. Gamble, may be illustrated by picturing a man in a boat by the side of a stream.

(I) The man may reach forward with a boathook, fasten it to some prominence like the root of a riverside tree, and pull the boat forwards; then loosen his attachment and quickly refix it farther ahead. This is the *pulling* method, and it is well illustrated by leeches and starfishes. When it is not swimming, but looping along over a stone, the leech exhibits the following sequence. Fixing its mouth and loosening the posterior sucker, it pulls its body forward, contracting its longitudinal muscles. At the end of this movement the posterior sucker has been brought forward almost to touch the margin of the mouth, and the body is arched steeply upwards like a croquet hoop. Then, the posterior sucker being fixed, the mouth is freed, and the body is protruded forwards to a new position of oral attachment. This protrusion is effected by a contraction of the circular and diagonal muscles, which, so to speak, squeeze the body forward. Then the mouth is re-attached, the posterior sucker is loosened, and the sequence recommences. The locomotion is often surprisingly rapid, and a land-leech can fasten itself to a man walking at leisure.

A starfish makes a number of its tube-feet tense with water by contracting the muscular ampullæ inside the arm; the suctorial tips of the tube-feet are pressed against the rock like so many firm fingers; some of the water from the tube-feet is then allowed to flow back into the ampullæ, so that a partial vacuum is formed between the tip of each tube-foot and the surface of the rock. Thus the tube-feet adhere firmly and a forcible pulling away of the starfish may break the tube-feet rather than loosen their attachment. The next step is a contraction of the longitudinal smooth muscles on the walls of the tube-feet, and this contraction pulls the starfish nearer to the points of attachment. Then by a strong contraction of the internal, somewhat syringe-like ampullæ, water is forced into the tube-feet at a pressure sufficient to do away with the partial vacuum and thus liberate the suckers. If the starfish is climbing up the face of shore-pool rock, it would slip back at this juncture were it not that

in the meantime another set of tube-feet have secured attachment higher up.

(II) The man may stand up in the boat and use a pole as a lever, pressing it backwards against the floor of the stream. By this "punting" he forces the boat forwards. This is one of the commonest modes of animal locomotion, being exhibited by all the diverse types that have firm appendages usable as levers against a firm base. A beetle hurrying across the roadway, a crab walking on the rock of the shore-pool, a frog jumping among the grass, an ostrich sprinting at full speed, a horse at a gallop, a man walking or running—all are using levers which propel the body forwards by pressing against a hard substratum. Sometimes there are complications, which do not essentially affect the principle of the method employed. Thus the freshwater mussel may make its flabby "foot" (a muscular protrusion of the ventral surface) tense with blood, close a sphincter muscle which prevents back-flow, and then pull the ploughshare-like organ backwards against the sand, thus pushing its body forwards. The foot has to be protracted by other muscles before the next step is taken. This method approaches pulling. Much in the same way the cockle takes little leaps on the firm sand.

The movements of snakes are somewhat intricate. A rapid dart forward may be effected by a sudden straightening of one or more of the bays of the sinuous body, but let us take the ordinary smoothly continuous progression, so remarkable in a limbless animal. Except in burrowing snakes, the ventral surface is covered by a single series of large scales, which can be raised and lowered. The posterior margins of these scales are sharp, strong, and imbricating. When they are raised, which is effected by special muscles, they tend to catch on the roughnesses on the ground. A snake cannot move on a perfectly smooth surface of glass or ice. Into the sides of the large ventral scales the lower ends of the ribs are attached by minute ligaments, and the upper ends are connected to the vertebræ by articulations which allow them to be very readily moved forwards and backwards. Several ribs are drawn forwards or headwards by muscles, thus moving the associated scales a minute distance headwards. A whole series of ribs and scales may be seen and felt working in the same direction at the same time. Then these same ribs are drawn backwards, with the result that the pressure of the raised scales against the hard ground pushes the body forwards. While one series of ribs is being drawn backwards, another series is being drawn forwards, and thus a continuous flowing movement is brought about. This case is, perhaps, intermediate between "punting" and "rowing".

(III) The man in the boat may stand in the stern and "scull", using a single oar to displace masses of water alternately to right and left. This is a common method among certain kinds of swimming animals, such as fishes and whales. In most fishes the swimming

organ is the post-anal body, which consists almost entirely of strong W-shaped blocks of muscle, dovetailed into one another, and centred in the backbone, which is very flexible from side to side. By an alternate bending and straightening of the posterior body, masses of water are displaced to right and left; and thus the fish is propelled forwards. In the case of Cetaceans the locomotion is similar, but a complication is introduced by the adaptive shape of the horizontally flattened flukes of the tail. In ordinary seals (Phocidæ) the hind-limbs are permanently turned backwards and bound up with the short tail, forming with it a unified functional propeller, for alternate lateral displacement of the water. The principle is the same in cases like sea-snakes and swimming leeches, where the gripping of the water and the using of it as a resistant mass, against which to contract, are not localised posteriorly, but extend over the whole length of the body. In sea-snakes there is usually a side-to-side flattening of the posterior region of the body.

(IV) Fourthly, the man in the boat may row, the principle being the *simultaneous* exertion of pressure on each side. Thus the duck-mole rows in the water with its webbed fore-feet, and the turtle with its paddles. Rowing in the air is the essence of flight in birds, bats, and insects, but the comparison with the boat must not be pressed, since the boat floats on the water, whereas the lightest bird has to expend part of its energy in keeping its body from sinking in the air. Brittle-stars (Ophiuroids) sometimes strike the sand with their posterior arms, and may be said to row themselves along on the solid; and in the mole's rapid turning in the ground, the fore-limbs are used like oars, as if the animal were rowing in the ground. Similarly the insect known as the Water Boatman (Notonecta) swims back-downward in the pool, using its long third pair of legs as oars. In many birds of the auk family the wings are used as well as the feet in swimming under water.

(V) The useful analogy of the man in the boat would become forced if applied to out-of-the-way modes of animal locomotion; so of these a few examples may be given. A jellyfish or a medusoid swims beautifully by alternately expanding and contracting the disc-like or bell-like translucent body. The rapid contraction drives the water out from the mouth of the bell, and the medusa or medusoid is propelled in the opposite direction. Cuttlefishes expand their mantle cavity or gill-chamber, and having filled it with water proceed to close it, by a remarkable hook-and-eye arrangement, so that the water cannot leave by the way in which it entered, but is forced, as the cavity contracts, through a narrow funnel. As the jet comes out with considerable strength, the body of the squid is driven rapidly through the water, with the head and the tentacles in the wash. The foremost part of the body is the top of the visceral hump. The same method of propulsion, by a posterior outgush of

water, is seen in larval dragon-flies; and it is interesting to notice that the violent expulsion of water from the posterior end of the food-canal is just an exaggeration of the gentle respiratory currents that are characteristic of these aquatic larvæ. Somewhat unusual, again, is the way in which lobsters and prawns jerk themselves tail-foremost in the water by suddenly flexing the posterior body (abdomen) forwards and downwards. This displaces a mass of water towards the head. On occasion the common scallop (Pecten), disturbed by an enemy such as the starfish, can jerk itself off the sea-floor with an energetic snap of its gaping shell-valves, and continue swimming for some time by snapping the two valves

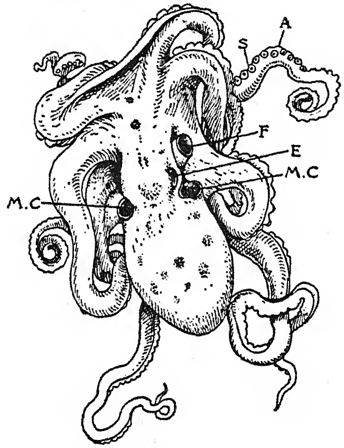


FIG. 41.

A Typical Octopus. A, one of the arms, with suckers (S). F, the funnel, through which water is forcibly ejected from the mantle cavity (MC), effecting locomotion. E, one of the eyes.

together. Somewhat more intricate and much more beautiful is the swimming of the nest-building Lima, a bivalve not uncommon in the Firth of Clyde and in similar places. In some ways the strangest mode of animal locomotion is exhibited by the common sea-urchin (Echinus) on a firm, flat surface. This animal habitually moves by means of its tube-feet, after the fashion of the starfish already described; and it also utilises its spines, which are swayed on ball-and-socket joints by basal muscles. But the Echinus is also able to tumble along on the tips of the five teeth of its "Aristotle's lantern", which project out of the mouth. The lantern can be swayed from side to side by powerful muscles, and the locomotion may be described, almost incredibly, as tumbling along on the tips of the teeth. The track shows at short intervals the indentations of

the five teeth, and the marks of spines in between. Perhaps this is the strangest of all modes of animal locomotion.

The movements of most multicellular animals are effected by means of muscles, and there is an important distinction between the unstriped or smooth muscle of sluggish animals, such as tapeworms, and the striped or striated muscle of ordinary active animals. It may be explained that unstriped muscle consists of homogeneous spindle-shaped cells, closely fitting accordingly between one another, each with a single nucleus. Ordinary striped muscle is made up of cross-striped cells much elongated, and usually with many nuclei, which are sometimes situated peripherally, as in man; sometimes embedded in the muscle-substance, as in the frog. A striped muscle-fibre is usually a much-elongated single cell; but in some cases a fibre seems to be due to the longitudinal fusion of a few cells. The most important general fact is that unstriped muscles are slowly contracting, and are therefore found in sluggish animals, such as Ascidians, and in the slowly moving parts of active animals, as in the walls of the food-canal, the walls of the bladder, the walls of the arteries, and the skin around the roots of the hairs. With these and similar exceptions, the muscle-fibres in ordinary active animals are cross-striped and quickly contracting. Some of the lower animals, such as Turbellarian and Nemertean worms, are aided greatly in their locomotion by superficial cilia. The last occurrence of these as locomotor structures is in newly hatched tadpoles, which, like larval lancelets, are richly ciliated.

Among unicellular organisms locomotion is effected by flagella, by cilia, by myonemes, or in an amœboid fashion. A flagellum is a thread of protoplasm, sometimes with an axial filament, and it moves in undulations. A cilium is alternately flexed and straightened, as one might bend one's arm at the elbow and elongate it again. It is of interest to notice that among multicellular animals cilia are very common, from the lowest to the highest, except in Nematodes or threadworms, where the abundant presence of chitin probably precludes their development. As has been mentioned, the Turbellarian and Nemertean worms are covered with cilia, which assist in locomotion; but above the level of these two classes, cilia cease to be locomotor except in larval forms, like the trochospheres of marine Annelids and Molluscs, and in rare cases like Rotifers, which are regarded by some zoologists as arrested larval forms. Starfishes and some other Echinoderms are peculiar in being richly provided with external cilia, but these are used for wafting food particles, not for locomotion. The big zoological fact is that above Nemerteans the function of cilia ceases to become locomotor, except in larvæ. They become of great internal importance, in diverse ways, for they may line a windpipe, an excretory tube, a female genital duct, and so forth. Myonemes are contractile

plasmic threads, anticipations of muscle-fibres, but intracellular. A familiar example is the axial filament that runs inside the non-contractile sheath of the stalk of the Bell animalcule (Vorticella). There are also good instances among the larger Sporozoa, which move sluggishly, probably through a contraction of the internal threads, which alters the shape of the cell and presses the firm cuticle against the substratum. To amœboid movement, probably the most primitive mode of animal locomotion, special reference will be made presently. In spite of its primitiveness, it is very intricate and difficult to understand.

CONTRACTILITY AND MOVEMENT

In the single-celled animals movement is effected (*a*) by protruding and retracting lobes or threads of living matter, as does the Amœba; (*b*) by the contraction of internal threads (myonemes), which are analogues of muscle-fibres, but within the cell; and (*c*) by the flexing and straightening of cilia, or by the undulations of flagella. Perhaps a fourth method must be distinguished in the sluggish movements of some of the corticate Sporozoa, which alter the shape of their cell and probably press the firm cuticle against the substratum. This may be sub-amœboid; yet in some of the larger forms, such as Gregarines, internal myonemes are clearly seen.

AMŒBOID MOVEMENT.—How many eyes must have watched the movements of Amœbæ since Roesel von Rosenhof studied them in 1755. He was by profession a painter of miniatures and, therefore, naturally interested in the minute. He tells us that he "frequently spent two or three hours in observing" what he called the "kleine Proteus"—the "Proteus animalcule", as it is still sometimes called—and, with a sharply pointed quill, he performed micro-dissection on the just visible animal, which is often about a hundredth of an inch in diameter. Large for a Protozoon, but small for a quill!

The Amœba's flowing along is the most primitive mode of living locomotion, yet uncommonly difficult to understand! It has been studied and pondered over by many naturalists, not only for its own sake, as movement before muscle, but because it persists in higher animals, as, for instance, in the mobile phagocytes that form a literal bodyguard, and in the microscopic tip of the fibre that grows out from an embryonic nerve-cell, as if feeling its way into the adjacent tissue. Here is a fine instance of conservatism in evolution—the same mode of cellular movement from Amœba to man!

To the ordinary observer an Amœba appears as a naked blob of living matter that protrudes blunt finger-like "pseudopodia", and draws them in again, altering its shape but not its volume, and flowing along the substratum at a variable rate that can be measured.

It seems to flow along or glide along, doubtless in some way gripping the substratum, but attentive observation shows that, at times at least, it is *rolling* along. For a definitely recognisable particle can be traced moving along the upper surface in the direction in which the Amœba is going, then disappearing over the front and, after a while, reappearing at the posterior end. There seems to be a "tank"-like or "caterpillar-wheel"-like movement.

The Amœba is anything but homogeneous; it is not like a drop of white of egg; it has zones in its living matter; it has a nucleus, contractile vacuoles, food-vacuoles and inclusions. It is a little

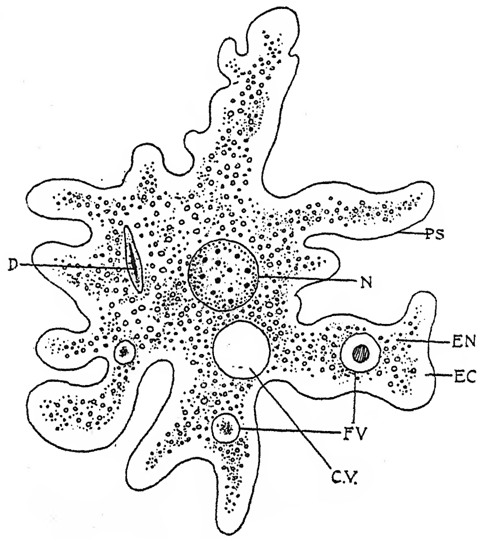


FIG. 42.

Diagram of a Common Amœba, about a hundredth of an inch in diameter. After Carter. N, nucleus with chromatin spherules; PS, pseudopodium; D, an engulfed diatom; EN, endoplasm or inner cytoplasm; EC, ectoplasm or outer zone of cytoplasm; FV, food-vacuoles; CV, a contractile vacuole.

world "der kleine Proteus"; and Prof. A. A. Schaeffer of the University of Kansas, who has been for many years a devoted student of amœboid movement, has been able to demonstrate an extremely thin outer fluid layer on the Amœba, a "plasma membrane" distinct from and external to the familiar outer zone or ectoplasm. Particles adhering to the plasma membrane may be seen moving forwards three to five times as fast as the Amœba itself. This extremely delicate plasma membrane is continually giving way at the anterior end of the Amœba, and being reinstated at the posterior end. It is probably the seat of surface-tension effects, and the tension seems to increase anteriorly and decrease posteriorly.

But, besides the movements in the plasma membrane, and apparently more fundamental, is a deeper protoplasmic streaming which is correlated with intricate physical and chemical changes, such as a rise in hydrogen ion concentration in an active outflowing. There are indications of rapid changes from "gel" to "sol" states, and back again. Yet when we think (*a*) of the relatively rapid movements in the plasma membrane with its surface-tension effects, and (*b*) of the deeper protoplasmic streaming, we are still far from having a connected picture of what takes place when one Amœba pursues another.

It is interesting to find that an Amœba, when comparatively free from external stimulation, moves in a sinuous path, in a very loose spiral; and Schaeffer has shown that many different kinds of animals, and man himself in swimming aimlessly, and all motile plants, like free-swimming Algæ, move in spirals of some sort, when moving idly, that is to say when the orienting senses are not functioning. At other times, of course, as when in pursuit of some booty, the Amœba shows a more direct controlled movement; and the unprejudiced observer will find it difficult to accept the view that it is entirely destitute of "purpose", ignorant though he may be of what "purpose" means at this low level of life.

Myonemes.—A clear and familiar instance of a myoneme or contractile plasmic thread is in the stalk of the beautiful Bell animalcule (Vorticella), which often grows in groups on the stems of water plants. It may be compared to a hand-bell borne mouth upwards on a long contractile stalk, and it passes frequently from an expanded phase with the stalk at its maximum length to a sharply contracted phase when it is drawn in close to its support. The sheath of the stalk is non-contractile, while the axial myoneme is like a thread of muscle; therefore the sheath has to coil into a spiral when the central thread contracts to a fraction of its maximum length. It is a fascinating sight, the sudden retraction, the momentary quiescence, the rapid shooting out again; and no one quite understands how it is done! Again there must be rapid alternations of "sol" and "gel" states.

Cilia and Flagella.—A cilium is a microscopic lash of living matter that is continually flexed and straightened again, as one might bend one's arm at the elbow and then straighten it out again. Cilia are especially characteristic of one of the orders of Infusorians, the Ciliata, well illustrated by the Slipper animalcule (Paramœcium), the trumpet-shaped Stentor, the bell-like Vorticella. Among multicellular animals cilia are also very common, from the lowest to the highest, except in the Threadworms and in the great phylum of Arthropods, where the abundant presence of chitin probably precludes their development. It is interesting to notice that the very simple Turbellarian or Planarian worms move mainly by means of

the multitudinous cilia that cover the surface of their body. Nemertean worms are also covered with cilia, but they have a highly developed musculature. A starfish is richly provided with external cilia, but they are used for wafting food particles, not for locomotion.

In short, after the level of the Turbellarians, the locomotor function of external cilia wanes, and its place is taken by muscles. But there are some exceptional cases of much zoological interest. The larvæ (trochospheres) of the marine Annelids swim actively by means of cilia. The same is true of the larvæ (trochospheres and veligers) of aquatic molluscs; yet when a young mollusc has no larval stage, but hatches out as a miniature of the adult, as is well illustrated by cuttlefishes, there are no external cilia. There is no doubt that ciliary

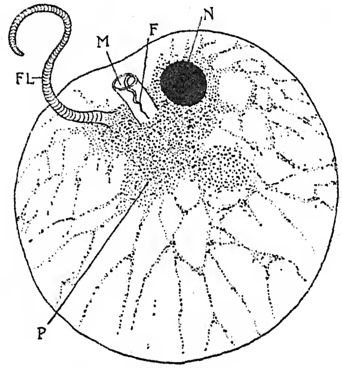


FIG. 43.

The Luminescent Night-light Infusorian, Noctiluca, which is about the size of a small pin-head. From a specimen. N, the nucleus; P, the much vacuolated protoplasm; FL, the large cross-striped locomotor flagellum; M, the mouth, raised too prominently, containing in its internal prolongation a small food-wafting flagellum (F).

locomotion is an old-fashioned feature, and it is interesting to find it at such a relatively high level as the larval lancelet and the larval frog. The newly hatched tadpole moves about by the cilia of its ectoderm. The peculiar little invertebrate animals known as Wheel animalcules or Rotifers, swim actively by means of cilia in front of the mouth, and in this connection it is interesting to notice the view of some zoologists, that Rotifers may be interpreted as relatives of Annelid worms which have remained permanently arrested at a larval level, though at the same time specialised there. But the big fact is that above the level of Turbellarian worms, with rare exceptions, cilia cease to be locomotor in adult life. They remain, however, of great *internal* importance in many types, as from covering the food-wafting gills of molluscs to lining the windpipe of man and other lung-breathing Vertebrates. They are

active in the interior of excretory organs, and they line the interior of the genital ducts of most female animals, thus aiding in the descent of the ova and even in the ascent of the sperms.

In animals with much chitin there seems not unnaturally something physiologically antithetic to the development of cilia. Thus they are absent throughout the Arthropod phylum, with perhaps the single exception of Peripatus, which has cilia in its kidney-tubes or nephridia. They are also absent in the Round Worms or Nematodes, which have a chitinoid cuticle, with perhaps the single exception of certain vibratile tags found in the lining of the female genital ducts.

What has been said of cilia applies also to flagella, which have an undulating movement, whereas cilia are alternately bent and straightened again. In sleeping-sickness organisms, which belong to the order of Flagellate Infusorians, a flagellum is expanded into an

FIG. 44.

A Single Smooth or Unstriped Muscle-cell, Slowly Contracting. N, the nucleus.

undulating membrane which extends along the whole length of the cell, and includes eight fine contractile threads or myonemes. At one end the flagellum projects freely. In this and in many other cases there appears to be some diffuse contractility throughout the whole unit.

MUSCLE.—There are two chief kinds of muscular tissue among animals. There is unstriped, smooth, plain, or involuntary muscle, which consists of homogeneous spindle-shaped cells closely fitting accordingly between one another, each with a single nucleus. These unstriped muscle-cells are found in sluggish animals, such as tape-worms and sea-squirts, and in the slowly contracting parts of animals, such as the walls of the food-canal, the walls of the bladder, the walls of the arteries, and the skin around the roots of the hairs. The zoologically important fact is that smooth muscle is slowly contracting, and thus more primitive. Its contractions are usually outside the control of the will, hence the term "involuntary", but

one non-striated muscle at least is "voluntary"—the ciliary muscle of the eye, so necessary for focusing on an object.

Ordinary "voluntary" muscle is made up of cross-striped cells much elongated, and usually with many nuclei, which are sometimes situated peripherally, as in man; sometimes embedded in the muscle-substance, as in the frog. A striped muscle-fibre is usually a much-elongated cell; but in some cases it seems to be due to the longitudinal fusion of a few cells.

Heart-muscle is involuntary, but cross striped, thus somewhat intermediate between the other two kinds. Its striæ are less marked than those of striped muscle, and each cell has a single nucleus. One cell is connected to another by terminal branches, and their boundaries are so vague that the whole is often described as a syncytium or coalesced grouping of cells.

Description of Muscle.—Though every biological student is familiar with muscular tissue, we venture to include here a very simple description of a piece of "flesh". When we look into a piece of flesh we see that it consists of a large number of contractile threads, the muscle-fibres, each complete in itself. In the biceps muscle of our arm, by which we bring the lower arm nearer the upper arm, there are about half a million of these muscle-fibres, each an engine condensed into a living thread.

Each living thread or fibre is an elongated cell, often about an inch long, but so slender, say $\frac{1}{500}$ inch in diameter, that it cannot be seen with the naked eye. There is a delicate elastic cell-wall (sarcolemma) enclosing a fluid living matter in which are embedded a large number of microscopic filaments or fibrils. These run the whole length of the fibre, and it is their contraction that contracts each fibre and so the whole muscle. Underneath the sarcolemma, which seems to insulate thread from thread, there are superficial nuclei at irregular intervals.

An ordinary muscle-fibre highly magnified has a cross-striped appearance, the fibrils showing alternate dark and light portions. Moreover, each light portion is crossed by a darkish line, and each dark portion by a light line, and we know that during contraction the light portion seems to be swallowed up, as it were, by the dark portion, which swells. Here we get a glimpse into the intricacy of the living engine, on the structure of which histologists are still far from agreed after wellnigh a century of microscopic endeavour.

In the process of contracting there is a shortening and broadening of each fibre and of the muscle as a whole, and as each fibre is connected with one of the many threads of a tendon or sinew that is fastened in most cases to a piece of skeleton, the result is drawing this nearer to or farther from another piece. In this way work is done. But this cold statement must be enlivened, if the contraction of muscle is to be appreciated. We must think of a bird like a swift

easily attaining to a velocity of a mile in a minute. The heron is no laggard on flight, but it strikes with its wings no more than twice in a second; we have to think of a bee with more than two hundred strokes in the same time!

THE CONTRACTION OF MUSCLE.—Now pressing the question farther home, we must ask *what happens chemically or biochemically when a muscle contracts.* Modern advance in this field began with the studies of Fletcher and Hopkins on the appearance and disappearance of lactic acid in muscle cells, and the associated explanation that the muscle fibre is a more or less permanent structure of parallel threads of protein, which tend to contract strongly if their surroundings become acid. It appears that the nerve-message to the muscle, "ordering" it to contract, causes lactic acid to be formed from some previous substance, and that this lactic acid by its mere

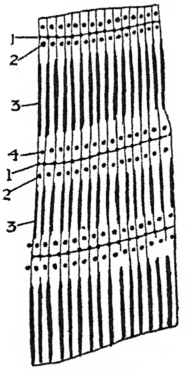


FIG. 45.

A Small Piece of Striped Muscle, showing the Fibrils. Note the alternation of longer dark (3) and shorter light bands (2–4); and a median line (1) across the middle of each light band.

presence causes the muscle fibres to contract; before the muscle can return to the normal again, the lactic acid has to be removed. The studies of Meyerhof, Embden, and A. V. Hill have greatly added to this part of the picture.

Lactic acid is readily derived from sugar, of which there is always a supply available in the muscle cell, which contains a store of the complex carbohydrate glycogen. The sugar does not exist free, but combined with phosphorus as hexose-phosphate; but from this combination lactic acid is easily liberated, and the fibre contracts. This, it must be noted, is done without the intervention of oxygen at all; the reactions are merely simplifications, not oxidations. The problem of removing the lactic acid now arises, although some is probably neutralised for the moment by the proteins present, and here oxygen does play a part. But the whole of the lactic acid

formed is not oxidised—a more economical arrangement is found: about one-fifth of the lactic acid is converted to carbon dioxide and water, and the energy furnished by these reactions is sufficient to reconvert the rest of the lactic acid into hexose-phosphate, its precursor, ready to be used again. The connection between the chemical energy of the oxidation of lactic acid and the physical work done by the contracting muscle-fibre is at first sight very indirect, nevertheless the latter depends entirely on the former.

In regard to all the bodily functions, it is important to think of them not only along the line of physiological analysis, but as they are expressed in everyday life. Their efficiency cannot be rightly appreciated unless the "Natural History" or ecological aspect is included. We would therefore refer to a concrete instance of the contractile or muscular function.

One of the most admirable of gymnastic feats among animals is the leap of the salmon. Against a rapid rush of water the fish hurls its heavy body into the air and surmounts a cascade many feet in height. To do this, it has to attain to a high momentum before it takes the actual leap, and we must notice how much of the posterior body of the fish is sheer muscle. The ratio of muscle to the total weight of the body is unusually high. One of the most remarkable leaps on record must be that shown in a photograph published by Dr. David Starr Jordan in *Nature* for January 16, 1926, representing a Pacific King Salmon (Chinnock or Quinnat) of about 25 lb. in weight, springing over the Punch Bowl Falls in the Cascade Range, Oregon, the height being about 30 feet!

NERVOUS AND SENSORY FUNCTIONS

As in other cases, we must restrict ourselves here to a few illustrations of the functions of the nervous system and the sense organs.

THE NERVE IMPULSE.—Few problems in physiology have been more debated than that of the nature of the nerve impulse. The sole of the foot is tickled, and a nerve impulse speeds up to the higher centres in the brain and spinal cord; a "reflex arc" is established and motor impulses come, by other nerve fibres, to the muscles of the leg; the knee is bent, withdrawing the foot from the irritation. The problem is, what goes on in the nerve-fibre when an impulse travels along it? English physiologists, notably Keith Lucas and Adrian, have done much to elucidate this question. They have shown, for instance, that the impulses in a single fibre are of constant strength; that is, if the fibre carries a message at all, it carries it at full power ("All or None" Law). Moreover, if an area on a fibre is weakened by anæsthetics, the impulse may, indeed, be choked off altogether; but, if it manages to struggle through the

region of "decrement", it immediately regains all its original power on entering the healthy part of the fibre on the far side. In man the impulse travels at a rate of about 300 to 400 feet per second; but in lower animals it may be much slower than this.

The behaviour of the impulse in regaining its full strength on the far side of a region of decrement led Keith Lucas to the analogy of a train of gunpowder, along which an explosion advances. Now it has been successfully demonstrated that in nerves, as in all living tissues, a process of "burning" continually goes on; oxygen is used up and carbon dioxide formed. Great difficulty has been found in proving that the amount of carbon dioxide produced is increased when the nerve is active, but Prof. G. H. Parker has been successful. Nevertheless, many workers have concentrated their attention rather on the electric currents ("currents of action") which appear when an impulse travels along a nerve; and as there is much to suggest that electrical forces are of primary importance in the *starting* of the nerve impulse, and in its transmission from one fibre to another, the chemical aspect of the nerve impulse has been somewhat neglected. Quite recently, however, A. V. Hill and his collaborators have clearly shown by means of an ingenious apparatus of great sensitiveness, that there is a definite production of heat by the nerve fibre in the transmission of an impulse. The amount of heat produced in one second's activity was about enough to raise the temperature of the nerve by one ten-thousandth part of a degree. If, as seems likely, this heat is produced by a "burning" process, it corresponds to the formation of a quantity of carbon dioxide closely approaching the quantity actually determined by Parker. It is plain that some sort of chemical activity accompanies the transmission of the impulse in nerve, but it is obvious that we are still far from understanding one of the most familiar phenomena of life.

REFLEXES

When we sit resting and thinking, with one leg swinging freely over the other at the knee, a sharp tap below the joint sends our dangling foot up into the air. This is the familiar "knee-jerk reflex", often used by physicians. What has happened when the rapid contraction of the muscles of the lower leg sends our foot up with a jerk? The mechanical stimulus of the knock has sent a thrill along sensory nerve fibres to the spinal cord; the impulse passes to connecting or associative nerve cells in the cord, and thence to motor nerve cells, whence, along motor nerve fibres, orders come to the muscles commanding them to contract. The brain is not required at all. A prearranged linkage of sensory, associative, and motor spinal nerve cells is sufficient in itself, with, of course, the muscle fibres, to give

effect to the motor orders. This linkage is prearranged for us before birth. It is part of our inheritance, and requires no learning or practice. What occurs is called by the physiologists an "unconditioned reflex"; and it is one of the commonest occurrences, both in man and beast. When we shut our eye at the approach of a missile; when we swallow what touches the back of our mouth; when we sneeze after a snuff; when we cough up a crumb that threatens to go down the wrong way; when we draw back our fingers from a hot cinder—we are illustrating various forms of unconditioned reflex, some more complicated than others.

When a sea-anemone closes its tentacles on a piece of food, when a starfish breaks off a pinned-down arm, when a crab breaks off a badly damaged leg, when an earthworm jerks itself into its hole if the ground vibrates under the blackbird's foot, when a snail draws in its horn at a touch, when a plaice puts on the colour of the sand on which it has come to rest, when a nestling opens its mouth at the touch of food in its mother's bill, we have to do with unconditioned reflexes; and the animal world is full of them.

It is characteristic of unconditioned reflexes that they are inborn, that they do not require to be learned, that they are shared by all the members of the species, and that they are often quite independent of the brain for their performance. It should be noted, however, that even in the case of a very simple unconditioned reflex like the knee-jerk we started with, a message goes to the brain to report the occurrence. Moreover, by an effort of will, if we are forewarned, we can prevent the straightening of the leg when the knock comes. The brain is sometimes able to suppress the normal reflex.

This suppression of a reflex used to be utilised in Oriental ordeals. Everyone knows that the presence of food in the mouth normally prompts a flow of saliva, which makes swallowing easier. But sometimes, under the influence of great sorrow, or fear, or some other emotion, we are unable to swallow, partly because the food remains so dry. Thus the suspected criminal in the East was given rice to chew, the somewhat ingenuous theory being that if he could salivate readily he must be innocent, whereas if he could not moisten the rice and swallow it he must be guilty.

A very valuable book, not easy reading, by the distinguished Russian physiologist, I. P. Pavlov, is devoted to "Conditioned Reflexes", which play an important rôle in human and animal life. Let us first of all explain how they differ from "Unconditioned Reflexes".

If a dog is shown a piece of flesh its mouth waters. If a whistle is always sounded when the flesh is shown to the dog an association is gradually formed between the sound and the prospect of a meal.

This association may become so strong that the dog's mouth will water when it hears the whistle, although there is no flesh in sight. The pseudo-stimulus need not be a whistle: sometimes a colour will serve. The flow of saliva in the dog's mouth illustrates a "conditioned reflex"; and this particular experiment, much elaborated by Pavlov, has the advantage that the strength of the reflex reaction can be measured by the amount of saliva secreted. Measurement goes to the core of science.

If a water-snail that has become accustomed to the biologist's ways has its mouth touched with a piece of lettuce it makes three or four munching movements. If the touch of lettuce is always accompanied by the gentle pressure of a glass rod on the snail's foot, an association is established; and after a hundred lessons the snail usually munches—at nothing—when its foot is pressed by the glass rod. It will answer back hour after hour—perhaps a hundred times—to what we may call the faked stimulus. The shadow works as well as the substance; and we need not smile too broadly at the snail, for we are ourselves frequent victims of the same trick, responding to a fictitious stimulus just as to the real one. But the snail forgets in ninety-six hours, whereas our enregistration lasts tyrannously. Think of our automatised reactions to the merely associative stimuli connected with rank, status, wealth—but we must not pursue this painful subject.

Let us think of ourselves more prosaically. To walk past some corners of Soho induces in many a salivary secretion; the savoury smell has become a trigger-pulling associative stimulus. It is sound physiology to put a menu outside the restaurant door; and on the Continent we have seen illustrative vignettes. To some susceptible people the sound of the dinner-gong at once brings about a conditioned reflex. It does not in the case of a stranger or a young child, since no individual association has been formed. The "conditioned" reflex, though it is usually based on some much older "unconditioned" reflex, is always built up in the experience of the individual. In mankind there is usually implied some appreciation of the meaning of the association, and that is probably true in many cases among the higher animals. A particular sound in the wood is followed by life-saving reactions, partly because of an intelligent reminiscent appreciation of the previous sequels of that sound. The higher wild animals are not fools; but we need not be surprised by the recent evidence that lions are not perturbed by the arrival of a motor-car against the wind. They have had no opportunity of forming associations with motor-cars. Among many of the lower animals the psychological aspect of the conditioned reflex is probably very dull. That is to say, there is very little awareness of any meaning in the secondary stimulus. In experiments, indeed, the connection between the secondary stimulus and the original stimulus may be quite

arbitrary or irrelevant. Yet we have found that tame mice in Aberdeen do not require more than fifty lessons to learn to congregate for a meal or a tit-bit when an electric bell is sounded. They then continue doing so for a considerable time, although there is no reward; and this is a "conditioned reflex".

In one of Jean Paul Richter's books there is a story of a humorist who put his teeth into a lemon just as the village whistlers were beginning to whistle on some joyous occasion. The result was inhibitory; yet the trick would not have worked if the members of the band had had no experience of lemons. A conditioned reflex differs from an unconditioned reflex in presupposing individual experience. There is no doubt that conditioned reflexes play a part in the behaviour of animals and also in our human affairs, but there is much more besides. There is often downright intelligence in animals, and to that man adds Reason.

Let us give an instance illustrating the subtlety of some of the reflexes. Physiologists have analysed what to many of us is a common experience, that emotion or mental effort alters the state of the skin. R. J. S. McDowall and H. M. Wells have shown that there is an elementary skin-constrictor-reflex or "psycho-galvanic" reflex, which may be brought about without co-operation of the higher nervous centres. The most noteworthy change is a fall in the electrical resistance of the skin, and this is shown to be the result of the constriction of the peripheral blood-vessels. This may be considered as part of the reflex arrangement by which an animal normally adapts itself to the anticipation of muscular exercise and defence. In man it may be instigated by a pin-prick, but also by a threatening movement. In other words, the stimulus may be emotional, not sensory. As the change in the blood flow affects the temperature sensations, there is a justification of such common sayings as "my blood ran cold" or "cold hands and a warm heart". The investigators notice that the reflex is associated with a diminution in the volume of a limb, as was previously demonstrated by Mosso and by Golla. Mosso pointed out that the volume of the limb changed in a student who passed from "seen" Greek translation to the greater mental effort of tackling the "unseen".

THE EYES.—In all the vertebrates, the structure of the eye is on the same general plan as the structure of an ordinary camera. It is a little dark box, into which light is admitted only from one side, through a system of lenses; these lenses focus the light rays upon a sensitive membrane at the back, the retina of the eye, which may be compared to the sensitive plate or film of the camera. The aperture of the lens, in the eye as in the camera, can be reduced when the light is especially bright; the eye, like the camera, can be focused for near or distant objects. But in sensitiveness, in adapta-

bility, in quickness of adjustment, in economy, if not in optical precision, the eye far surpasses any camera.

The surface of the eye, where it looks out upon the world, is protected by a delicate membrane called the *conjunctiva*; behind this is the *cornea*, a transparent window in the thick, opaque white outer wall of the eyeball. Behind the cornea is a small space filled with a clear fluid, the *aqueous humour*, and behind this is the *lens*, a flattened sphere of glass-clear protein. But in front of the lens, as everybody knows, lies the *iris*, a thin ring of opaque tissue which appears blue unless it happens to contain brown pigment. The iris can contract or expand, so that the aperture it surrounds, the pupil, may be small or large; in this way the amount of light entering the eye proper can be controlled. Behind the iris and the lens is a fairly large space, comparable to the box or bellows of a camera, but filled with a clear jelly, the *vitreous humour*. The wall of this chamber is lined by the sensitive membrane, the retina, which receives the light-rays and translates them into nervous impulses which pass to the brain by the optic nerves.

The eyeball is mounted upon a ball-and-socket joint, elaborately cushioned and sprung, and its movements are controlled by six muscles. Four of these run from the wall of the orbit to the equator of the eyeball, and, when they contract, act like reins, pulling the eyeball round in one direction or another; the other two are shorter and oblique, and serve to balance and restrict the action of the "reins". As everybody knows, there is the closest correlation between the eye-muscles on the two sides of the body; the eyes move together, with the most delicate adjustment, to ensure that their axes shall converge upon the object looked at, be it near or distant. The external muscles of the eyeball are excellent objects for the study of co-ordination in muscular movement, brought to its highest pitch.

The iris is also muscular, so that the dimensions of the pupil may be varied. When a bright light shines into the eye and stimulates the retina, a reflex comes into action and causes the circular muscle of the iris to contract, thus diminishing the size of the pupil. When the light stimulus is removed the pupil dilates again, and in absolute darkness remains dilated; but if any light remains, the pupil gradually contracts as the eye becomes used to the dim light. In this reflex, too, there is great correlation between the two eyes; a light shone into one eye causes contraction of both pupils.

The eye differs from a simple camera in its optical system, for it has two lenses—the "lens" proper, behind the iris, and the "cornea" in front, and the latter is the more important of the two in refracting light rays. But in fishes, or any other vertebrate which may happen to find itself under water, the whole work is done by the lens; the cornea can only refract light rays when they come to it *through the*

air. Moreover, there is a special fascination for the physicist in the properties of the lens; it has greater refractive power than its composition and shape would suggest, because at the centre it is not merely thicker but also *denser* than towards the circumference; and, finally, it has in birds and mammals the power of changing its shape for the purpose of focusing. In fishes, amphibians, and some reptiles, as in some invertebrates, the eye focuses as a camera does—the distance between the lens and the retina is altered, by one means or another; but in other reptiles, in birds and in mammals, a new principle has been discovered. A lens, removed from the eye, has the shape of a much-flattened sphere; but in position it is compressed by the ligaments which hold it, is still more flattened, and is then able to throw sharp images of *distant* objects upon the retina. When we look at near objects, however, by the contraction of certain muscles the pressure of these ligaments is eased and the lens is able to approach its natural shape, thus altering the focus. This power of accommodation of the eye is surely of some service in judging distance; it becomes noticeably lessened with advancing age.

Distance-judging is effected by one eye partly in this way, by the two eyes in conjunction, partly by judgment of the amount of deviation from the parallel between the axes of the eyes—up to the point where it requires violent internal squinting to see with both eyes a smut on the tip of the nose—and partly by subtle appreciation of the differences between the images on the two retinæ. But experiment shows that in ordinary life rapid, experienced judgments of the meaning of the apparent size of objects, of relative movement, of light and shade, and of perspective play a very great part in our judgment of distance.

The retina, the sensitive membrane itself, is very complex in structure, despite its thinness. The light which falls upon it has to traverse a network of nerve-cells and nerve-fibres before it reaches the layer which we know to be the receptive surface. This layer is known, from the shape of the cells of which it consists, as the layer of the rods and cones; and a careful weighing of indirect evidence enables us to form a theory of the meaning of these structures. It is supposed that the cones are the cells which receive images in bright lights, and that they alone have the power of discriminating colours; while the rods are used in twilight vision, for seeing in very dim lights, and are colour-blind. In some way associated with the rods is a pigment, the "visual purple", which is bleached by light. It is supposed that in night vision this bleaching of the visual purple means the production of some new chemical substance from the pigment, some substance which acts upon the rods and stimulates them to send impulses to the brain. We must almost inevitably assume the existence of some other substance which in a similar way stimulates the cones, a temporary translation of light-energy

into chemical energy being the most plausible "explanation" of vision; but when we remember that the cones can discriminate colours, we must go farther and assume that there are at least three of these imagined substances, one for each of three primary colours!

The sensitiveness of the retina is amazing. The amount of light-energy required to evoke a response from it has been measured, and found roughly equal to the amount of light-energy which would, under ideal conditions, enter the eye in one second from a candle burning five hundred miles away. The retina is two or three thousand times as sensitive as any photographic plate or film.

The retina is not perfectly uniform. In the centre, on the line of the axis of the eye, is a small depression, the "yellow spot". Here, the overlying layers of nerve-cells are thinned out; rods are absent, and only cones are found—adaptations, as we may well suppose, for increasing the sharpness of sight at the point where it is most required. Further from the centre, towards the edges of the sensitive area, of which we make less conscious use, the number of rods relatively to the cones steadily increases.

Armed with this conception, we can perhaps better understand the familiar phenomena of "dazzling". As everyone knows, when one comes from a dark room into bright light the sight is confused for some moments, in spite of a powerful constriction of the pupils. Very soon, however, the eye becomes "light-adapted", and vision is clear again. Again, we know that on passing from the light to the dark we are at first unable to see anything; but after a time the eye becomes "dark-adapted" and objects are easily recognised. In this case it seems that two processes play a part: first, the cone mechanism has to be shunted out of action, and it takes a moment or two for "after-images" in the cones to die away completely; secondly, the rod mechanism has to be brought into action, and this probably involves the formation of a supply of visual purple, which takes time. The dark-adapted eye is excessively stimulated by bright lights, which again means that some time must elapse before the rod mechanism is shunted out of action. It may not be too fanciful to regard the rod mechanism as a sort of "low gear" which can be brought into use when conditions are too difficult for the cone mechanism to work successfully. But the cone mechanism itself can be fatigued by prolonged exposure to too bright a light, so that a dark cloud seems to obscure vision for some moments; it is interesting that if the bright light is coloured, other colours can be clearly seen immediately with no sign of fatigue—a fact which supports the view that there are in the retina different mechanisms for several different primary colours.

The question of colour-vision in the lower animals has been much discussed and investigated by many different methods. Very careful experiments have conclusively proved that honey-bees and probably

many other insects can certainly distinguish and remember colours, and that the colours of flowers are of real significance to their insect visitors; though the insect's range of colour sensations is not the same as ours. All the vertebrates appear to have some power of seeing colours, yet it has proved very difficult or impossible to teach even the intelligent dog to associate any meaning with a given colour, so that we must admit at least that colour-sensations play only a small part in the dog's mental life.

The axes of the eyes of a man, or of a cat, or of an owl, are almost parallel, and the two visual fields overlap very greatly; nearly everything that is seen is seen with both eyes. But many mammals and most birds have their eyes set on the sides of the head, the axes widely divergent, and only in a narrow angle directly in front of the head (in some birds, directly *behind* the head also) can objects be seen with both eyes simultaneously. They have lost something in accuracy of vision, especially in appreciation of distance, but they gain by being able to keep constant watch on all sides. It is interesting that it is typically the hunted animals, such as the antelope and the hare, which are best protected against stealthy attack; while the hunters, such as the carnivores and the birds of prey, can focus both eyes upon the quarry. But all animals, even those with eyes farthest apart, and even those which, like the chameleon and the flat-fishes, can move their eyes quite independently of each other, appreciate the advantages of binocular vision, and will bring both eyes to bear on any object that attracts their attention.

THE EVOLUTION OF SIGHT.—When one thinks of the human eye or the eagle's eye, and of the vision that both enjoy, it is difficult at first to silence the feeling that these structures and functions are much too wonderful to have been evolved. But this is a fallacious impression due to unacquaintance with the graduated series of stages that lead up to the end-results. In regard to human inventions, the final approximations to perfection would often seem magical, if one did not know something about the long series of antecedent tentatives. So is it with what may be called Nature's many inventions. The most evolved eyes are miracles of adaptiveness, but the first light-sense organs are mere pigment spots; and the stages are many and gradual that lead from these to the compound eyes of the butterfly, along one line of evolution, to the single-lens eyes of cuttlefishes on another, and to the eyes of backboned animals on a third.

Two other general points should be noted—(1) that the stages in the evolution of the optical instrument must be correlated with the gradual improvements in the brain to which it sends tidings; and (2) that the eye had many functions before it became an image-forming or a picture-making organ. Just as the ear was for millions

of years a balancing or equilibrating organ, before it became a hearing ear, so the eye was for ages a light-and-shade organ, or a movement-detecting organ, or something else, before it could be said that its possessors were able to form a picture of their surroundings. That power came very late.

The electro-magnetic radiations that we call light have many direct effects on living creatures. Thus they bring about photosynthesis in green plants; they evoke pigment-formation in many animals; and they seem to have a tonic influence on growth and health. But by light-sense is meant a special photochemic susceptibility of certain receptor nerve-cells to light-rays in general or to certain light-rays in particular, with the result that the explosive thrill, evoked by the absorbed rays, is passed on to other parts of the organism which react in some definite way, notably by movement. The living matter of a simple Unicellular animal or Protozoon may be sensitive to light, without there being any appreciable differentiation of structure that could be dignified even with the name of "eye-spot". The function comes before the organ! But one of the first progressive steps was the accumulation of a little splash of pigment, which may have various uses—for instance, in absorbing rays to which the receptor cell or protoplasm is not attuned, or in surrounding the sensitive spot so that the light enters only from straight in front. A second step was the formation of something in the way of a lens which focuses the rays of light. In the simplest cases the lens is not even cellular, so primitively do things begin! A third step was the fashioning of the "light-organ" into something like a little cup or camera, with the receptor cells on the posterior concave surface and the lens in front. In some of the sea-worms, for instance, we start with diagrammatically simple "cup-eyes", like prentice-work, and gradually pass to very elaborate "cup-eyes", the grading of the series being in itself a quite convincing "evidence of evolution".

With the development of a minute optic skin-cup, so readily brought about by inequalities of growth, there must be associated (*a*) the beginning of the perception of the direction from which the light comes; (*b*) the first dim awareness of moving objects whose shadows flit across the sensitive wall of the tiny camera; and (*c*) the first experiences in the visual detection of obstacles. But long before animals showed directed movements, definitely oriented in relation to the light-stimuli, there were vaguer reactions. Thus many animals, such as tube-inhabiting worms, sea-urchins, rock-barnacles, gnat larvæ, burrowing bivalves with their siphons projecting out of the sand, and the long-horned snails, answer back by reflex retraction to the shadow of one's hand held ever so gently above them. Many do this, although they have no eyes in the ordinary sense of the term. It should be noted that the shadow-

reflex is never exhibited more than a few times within a short period; the creatures soon cease to answer back.

Much less frequent than reaction to a shadow is reaction to a sudden increase of light; but there are instances of animals that move towards the more illumined part of an aquarium lighted from above, though a reverse movement is commoner. Our point is simply that long before there was any "seeing" there was exquisite sensitiveness to light and shade. This discrimination is of obvious importance to animals that live in darkness or are active at night, as also to others which cannot be active except in the light. Of great interest, in insects especially, is the relation between the intensity of the illumination and the tone of the muscles; but this is a very difficult question.

When a simple animal moves from an illumined to a shaded part of an aquarium lighted from above, or conversely, it is illustrating the light and shade reflex; but a higher level of reaction is seen when an animal moves towards or away from the source from which the light comes. This "phototactic" movement usually implies something in the way of a genuine eye; yet it is sometimes exhibited by creatures that have not risen to anything higher than an eye-spot. In certain cases there is no actual movement from one place to another, but merely an adjustment of the body so that both sides are equally illumined, or equally in the shade. But it was a great step when the eye began to be used like a compass, enabling the animal to steer, either automatically or tentatively, towards an illumined object. In other words, it was a great step when sight became directive. It is very instructive to contrast the circumambulating, circuitous track of an animal moving in total darkness with the straight course it pursues when there is an illumined object to serve as a guiding star.

The next great step in eye evolution was the formation of an image, the visual perception of form. This implied the differentiation of a lens and a retina, and not too simple a retina. Towards the seeing of shapes there were doubtless many steps, such as the perception of moving objects without discrimination of their precise form, and the recognition of obstacles in the path without perception of their precise contour. Of much importance must have been the evolution of some method of accommodation, that is to say, some way of adjusting the focus of the eye for objects at different distances, or for the variously distant parts of the same object. This may be effected by altering the distance of the lens from the retina, as is illustrated by marine worms, the sea-snails called heteropods, the cuttlefishes or squids, most of the true fishes, and the amphibians. In reptiles, birds, and mammals the method is quite different, for accommodation is effected by altering the curvature of the lens.

After a certain stage was reached, probably among the worms, the evolution of eyes proceeded along three distinct lines. There was the line which finds its climax in birds and mammals. But quite different in detail and in development is a type of eye found among molluscs, and reaching a climax in the extraordinarily effective eyes of octopuses and their relatives. Entirely different again, and occupying a place by itself, is the compound eye of insects and higher crustaceans, where there are hundreds of lenses and hundreds of percipient retinules, the image formed being a mosaic built up of numerous minute contributions. This type of eye seems better adapted to the detection of movements than to the perception of form.

The story of the evolution of vision should take account of the movements of the eyes, the binocular apparatus, the discrimination of colour, and the general improvement in picture-forming. The last depends mainly on the size of the instrument, the number of sensitive receptors in the retina, and the number of nerve-fibres passing from the receptors to the brain. Nor can we forget the evolution of the brain behind the eye; for it is the brain, with its mind, that changes vital photography into intelligent scrutiny, and sublimes sight into vision. The eye sees what it brings with it, the power of seeing, as we all prove every day, both pleasurably and painfully.

Photoptic Sense in Earthworms.—How does an earthworm know when it is time to come out of its burrow?—for it has no eyes. In the strict sense, perhaps, it does not know anything; therefore our question becomes: how does it sense the difference between light and darkness? The earthworm is constitutionally a light-shy animal, as technical people say, negatively heliotropic. Those earthworms that we see above-ground during the day are out of health, or drowned out of their burrows, or parasitised by some fly. But let us keep to our question: how is the earthworm made aware of differences of light and shade? It is a familiar fact that there are numerous sensory nerve-cells in the earthworm's skin which send tidings of various kinds from the outer world to the nerve-cord. But Dr. Walter N. Hess has found a special kind of superficial cell which is sensitive to light. It does not seem to have been noticed before, though hundreds of zoological students are studying microscopic sections of earthworms every year. Each of these special cells, according to Dr. Hess, has a central glassy body like a miniature lens, and this is surrounded by a network of nerve fibrils which will act like a little retina. These cells are most abundant in those parts of the earthworm's skin that are most sensitive to light. They are absent from the under surface of the rings except at the two ends of the body. Similar "photo-receptors" are well known in leeches, which are exquisitely sensitive to light and shade.

It is important to keep in mind the interesting fact that before the eye became in the course of ages a seeing eye, able to form an image, it was a structure for distinguishing between light and darkness; and that is the level represented by these scattered "photo-receptors" of the earthworm. Similarly, before the ear became in the course of ages a hearing ear, it was a balancing organ, as it continues to be. And before the brain became a thinking organ, it was the organ for controlling muscular movements.

Sense of Light without Eyes.—Earthworms have no eyes, yet they are very sensitive to differences of light and shade. Various blind or blinded insects, both adult and larval, are known to react to light. Some investigators have spoken of a "dermatoptic sense", meaning that the general surface of the insect's body is sensitive to light. In this connection some striking experiments on entirely blinded minnows have been made by Scharrer, proving reactivity to light after the complete removal of both eyes. They put on dark colour when illumined; they assumed a light colour in darkness. In an aquarium constantly but faintly lighted, a stronger light was turned on shortly before and during each meal, and the blinded minnows established a conditioned reflex in a few days, and when the light was turned on would snap and jump about in search of the food even when there was none. This reactivity was found to have its seat in a region of the head corresponding to the optic thalami of the brain—the region from which the paired eyes grow out. This region also gives origin to the parietal organ, which has an eye-like structure in some reptiles, notably in the New Zealand lizard or Sphenodon. The parietal organ is in a very primitive state in bony fishes, and its extirpation does not affect the blinded minnow's reactions to light. It is the whole region of the optic thalami that is important as a seat of sensitiveness to light, and a remarkable feature is that it responds to very slight illumination.

Eyes that Shine in the Dark.—Why do a cat's eyes shine in the dark?

Part of the answer is that the question is not rightly put. When we see a cat at night with shining eyes there is always *some* illumination, such as a candle or a street lamp. There must be some rays from somewhere, for there is no production of light in the eyes. The real puzzle is: Why do the cat's eyes give forth a light much more brilliant than that of a candle or a lamp?

The next step is to notice that the cat is by no means the only animal that has eyes which shine in the dark. If we open the door of a dark stable in which there is a sheep we see the same shining eyes. The peculiarity is shown by some other mammals, and the eyes of various moths, like the death's-head, shine in the dark. So do those of many beetles. When the light of a lamp falls sideways on the eyes of the big rhinoceros beetle of Ceylon, its eyes shine out

like brilliant rubies. In some of the moths the colour is red, in others golden yellow. Thus our question comes to be: What is there in common between the cat's eyes and the rhinoceros beetle's eyes that both should "shine in the dark"?

The answer is that both have a reflecting layer in the back of the eye. This reflecting layer—called the tapetum—acts like a concave mirror, and sends out again the scanty rays of light which have already entered through the lens. As the light-rays pass out again through the lens they are concentrated, and thus appear more brilliant than the original source of illumination. In a pocket electric torch the incandescent filament gives of itself no great light, but when passing through the lens the light is concentrated and strengthened.

In the eyes of the cat and the beetles the light comes, to begin with, not from within, as in the electric torch, but from without, from the lamp. In the cat the reflecting mirror consists of flat cells filled with microscopically minute crystal-like spangles; in the moth the mirror is formed by a network of air-tubes similar to those which take air to every hole and corner of the insect's body. It is interesting that these reflecting mirrors should be made in two quite different ways.

What can be the use of having eyes that "shine in the dark"? It is not likely that it can be of use to reveal the cat's presence! The answer is that if it were *quite* pitch dark neither cat nor death's-head moth nor rhinoceros beetle could see at all; but it is very seldom so dark as all that—there is usually some faint illumination, even at dead of night.

So the ingenious suggestion—it is only a suggestion—has been made that the reflecting of the faint rays of light from the back of the eye forwards again gives the sensitive cells of the eye a "second impression", a second chance to see something. It is a very interesting question.

THE BIOLOGY OF TEARS.—There is an interesting desert lizard in Mexico and California that goes by the name of Horned Toad or Phrynosome. It is a non-aggressive creature, asking only to be left alone, but it becomes greatly excited when it is teased. It is said to shed tears of blood, and this is in a remarkable way the case. When it is much perturbed, there is a rush of blood to the head, and the eyelids become so much congested that they swell to twice or thrice their ordinary size, and from below the upper one there issues a fine jet of blood! There is a superficial hæmorrhage, occurring under very unusual circumstances, and it is such an expensive mode of weeping that we cannot wonder at it being unique. It corresponds in part to a man's eyes becoming blood-shot in a rage, and it throws from a distance some light on weeping.

Just as with laughter, so in regard to tears, we must not think

first of the sophisticated human reason. For a number of mammals shed tears copiously, and the primary reason must be relatively simple.

In Darwin's *Expression of the Emotions*—a book far too little read—some facts are given in regard to the weeping of some monkeys and the Indian elephant; and other cases are known, without including "crocodiles' tears", which seem to have been exaggerated.

It is a familiar experience that a flow of tears may follow a strong scent, a blow, irritant particles in the eye, exposure to intense cold and, in short, a great variety of stimuli. What happens is an exaggeration of the normal secretion of the lachrymal gland, whose ordinary function it is to moisten the surface of the eye (the conjunctiva).

Our tears issue from several ducts on the inner surface of the upper eyelid, and some of them are caught by a small aperture in the lower lid and pass through the lachrymal sac into the nasal passage. The others, as we are all aware, overflow and roll down our cheeks.

The exaggerated secretion may clear the eyes, which is always advantageous, even if you wish to give a kiss for a blow; and the tears may also have their utility in the nostril, e.g. in increasing olfactory sensitiveness. And apart from utility the exaggerated secretion comes as a relief to changes in the blood-pressure and musculature in the region of the eye and its glands. We must recall the Phrynosome "weeping blood".

It is not unusual to see strong men weeping copiously at a comedy, even in response to stimuli so different as Sir Harry Lauder and Prof. Leacock. We have seen people laugh till the tears rolled down their cheeks; and there is also something almost sacred in "tears of joy".

Very young children cry vocally long before they shed a tear, and Darwin found that a frequent age for the first true weeping was about three months.

The flow of tears in early childhood may express pain and distress, but it is often worked towards by a fit of screaming that expresses vexation at some thwarted wish. Later on, the weeping is gradually inhibited until it is only evoked by very deep emotion. In many cases the muscular contractions associated with profuse weeping in children may be seen in strongly emotionalised adults, although the supply of tears has long since ceased.

Although Darwin credited some mammals, like monkeys and elephants, with a capacity for copious tears, he thought this was absent in the anthropoid apes, and this is borne out by recent observations. In his striking book on the *Mentality of Apes*, Prof. Köhler distinctly says that he never saw one weep. Their

expressions of grief are undoubted, but these are not associated with tears. The fact that weeping seems to require some practice in young children is in harmony with Darwin's conclusion that the habit "must have been acquired since the period when men branched off from the common progenitor of the genus Homo and of the non-weeping anthropomorphous apes".

Some races weep much more readily than others, as may be noticed among sailors and soldiers under very severe exposure, but this is an intricate question. The more emotionalised types will tend to weep more readily. but this may be counteracted by habituated control.

According to Darwin, the origin of weeping in the individual child is to be found in the gorging of the blood-vessels of the eye as the result of prolonged screaming, this being due to pain or hunger or the like. The gorging of the blood-vessels of the eye is associated with a contraction of the surrounding muscles and with other effects which react reflexly on the lachrymal glands and induce exaggerated secretion of tears.

On this view, crying is primary, and weeping is a secondary consequence. It is not of great physiological use, perhaps, for it is not without justification that we speak of "idle tears"; and yet it has been racially justified as a safety-valve which lessens congestion and may actually relieve pain. In all probability, however, the biology of tears requires another chapter, which will disclose the influence of some hormone, such as adrenalin, which has such a notable influence on the tone of the muscles, the blood-pressure, the breathing-movements, and so forth. It is well known that an extra supply of adrenalin follows an emotional storm, like that of anger. The sympathetic nervous system is excited; the thrill passes to the suprarenal bodies; more adrenalin is produced and rapidly distributed throughout the body by the blood stream. We know that the cat's hair stands on end automatically in an emotional gust induced by an obtrusive dog: so it may be that our tears have a similar emotional-endocrinal factor.

THE HEARING EAR.—It is usual and convenient to consider the organ of hearing under three heads: the outer ear, the middle ear, and the inner ear. The first two are simple enough; but the inner ear is a complicated system of tubes and bulbs and canals, appropriately called the labyrinth. But the greater part of the labyrinth has to do with the sense of balance, and not with hearing at all; it is not to be considered under this heading.

To understand the organ of hearing at all, it is necessary to understand the nature of sound, which is a vibration transmitted by molecules, usually in the air, but equally well in water or in solids. When a taut violin-string is plucked, it emits a note; that

is, it sets up a series of vibrations in the air. These vibrations have a certain violence or amplitude, determining the *loudness* of the sound. Further, they have a definite tone or *pitch*, the wave-length of the vibrations, which is determined by the quality, thickness, and length of the string. A similar string of half the length will emit vibrations twice as rapid, that is of half the wave-length, and we say that the note produced is an octave higher than the first one. But a plucked string vibrates not only as a whole, producing the characteristic or fundamental tone, but vibrates also and simultaneously as two halves, and three thirds, and so forth, producing simultaneously the "overtones", an octave, an octave and a fifth, two octaves, and so on, above the fundamental note. Different means of producing sound differ in the strength of the different overtones produced; and it is these differences, in the distribution of emphasis among the overtones, that give to each musical instrument, or to any heard note, its characteristic *timbre* or quality. The differences between the various vowels of speech are primarily differences of timbre, that is, differences in the number and strength of the accompanying overtones. A *noise*, as distinct from a note, is a jumble of vibrations of different pitch and timbre.

The outer ear in mammals consists of the externally visible flap or *pinna*, which is probably almost useless in man, but in many other mammals serves as a funnel to collect sound and, being movable, to locate sounds. From the pinna a passage leads through the wall of the skull, and is closed at the inner end by the delicate "drum" of the ear, which is thrown into vibrations by sound-waves.

The middle ear acts as an amplifier, to magnify the vibrations received by the drum. The vibrations are carried from the drum by a chain of delicately poised little bones, called the hammer, the anvil, and the stirrup, to a similar delicate membrane which closes off the inner ear. As this inner membrane, the "oval window", is much smaller than the drum of the outer ear, the vibrations are concentrated or strengthened in passing from the one to the other, in spite of a certain loss of energy in friction. The middle ear itself is merely a cavity, bridged by this chain of little bony levers; the cavity communicates with the pharynx by the Eustachian tube.

Of the inner ear, the only part which has to do with the sense of hearing is the *cochlea*, which is a tube coiled in a spiral. Within this tube, which is full of liquid, are transverse membranes and a complex arrangement of sensitive and supporting cells—too complex to be easily described, especially since the meaning of the complexity is unknown. The generally accepted theory of the nature of the process of hearing is that it depends on the resonance of the fibres of one of the membranes. This, the *basilar membrane*, consists of a very large number of fibres, some twenty thousand or more. It is supposed that these fibres are so graduated in size and shape that

each one corresponds to a particular note, as a violin string does; and that when that note reaches the ear from outside, the appropriate fibre vibrates in sympathy, or by *resonance*, as it is said, and that this sympathetic vibration causes impulses to be sent to the brain and there interpreted. It is well known that if a note is sounded beside a piano, the appropriate string of the piano will vibrate and sound in sympathetic resonance.

One of the most striking confirmations of this theory is given by experiments in which guinea-pigs were exposed for weeks at a time to the sounding of particular notes on an organ-pipe. It was then found by examination that specific regions of the basilar membrane had undergone degeneration, and that the region affected varied with the note sounded.

It is rather difficult to compare the hearing organs of lower animals with those of man. In mammals and birds the sense of hearing is certainly well developed, sometimes better than in man, so that vibrations over a wider range may be detected (the human ear detects vibrations between 40 and 40,000 per second, roughly, but cats and dogs are certainly sensitive to much shriller notes). But in lower vertebrates and invertebrates it is not easy to be clear about the definition of "hearing". If a fish is sensitive to vibrations of similar frequency in the water, is that the same thing as "hearing" vibrations in air? And if so, is the sensitiveness of an earthworm to vibrations in the surrounding soil the same thing again, or is this to be classed as a different sense? The sense of hearing and the sense of touch are closely allied, and it is hard to draw the line between them and say, This shall be called hearing, and this not. But in some insects at least an indubitable sense of hearing exists, and it is interesting to notice that it is best proved in those species in which one or both sexes has the power of producing some sound at will. Insects have no true voices, but many can produce notes by rubbing roughened parts of their hard cuticle together; in some cases elaborate fiddle-like instruments have been evolved; the trilling of the grasshopper is familiar to all.

THE SENSE OF BALANCE.—There are many different kinds of animals that have ear-like organs and yet we have no evidence that they can hear. In other cases where the ear-like organs are put out of action, it makes no difference to the sense of hearing, if that is present. What then is the meaning of the ear-like organs found in myriads of backboneless animals? The answer is that they are balancing or equilibrating organs, by means of which their possessors automatically adjust their body so as to keep their balance in swimming, flying, or running, or even their pose when resting. If the organ is injured the animal will often tumble about anyhow or swim on its back. A common type of an ear-like organ is a little bag filled with fluid into which there project the fine hair-like pro-

longations of sensory cells. Suspended in the fluid there are fine particles of lime secreted by the wall of the sac, or particles of sand and the like introduced from the outside world. These particles jostle against the sensory hairs when the fluid is made to oscillate by movements of the body. Among backboned animals the hearing of the ear becomes more and more pronounced as we ascend the scale; but even in man the balancing function of the ear is still very important.

A SENSE OF DIRECTION?—Some very clever men are singularly deficient in what is popularly called a sense of locality. Time after time they visit the same town or the same big building without learning in the least how to find their way about. In cases we have known, the defect is associated with exceptional intellectual ability, and possibly indicates that the mind is preoccupied with great problems, and that the habit of attending to topography has never been formed. On the other hand, we have known very gifted men who could find their way without a compass on a moorland shrouded in mist. They had indeed served a long apprenticeship to way-finding, and were what might be called objectively-minded, but at a juncture their only stipulation was that there should be no talking.

Many a man can walk from the railway station for an hour into the heart of an unknown city, and then retrace his steps without mistake and without giving the matter much attention. In such a case there is probably an unconscious registration of landmarks and also some general registration of the muscular movements performed. The useful habit that many people have of orientating themselves in every new place must prevent big errors, but it is necessary to distinguish the deliberate attending to details from the almost automatic retracing of steps.

Many very careful experiments have been made with ants, and Rabaud has summed up the evidence in his book, *How Animals Find Their Way About* (1928). His examination of the well-established facts, excluding all hearsay, is entirely against the postulate of any mysterious sense of direction. An ant has an instinct to return to the nest with its treasure-trove, but it finds the way home by serving an apprenticeship.

In contrast to its instinctive activities, which depend on inborn ready-made capacities, the ant *learns* its way about. There is, of course, no difficulty when it gets on to a well-trodden ant-road, such as often exists, for then the olfactory traces are probably in most cases sufficient; the problem is in regard to pathless territory. The probability is that the ant gradually builds up a general impression of the area around the nest—a general impression consisting mainly of visual cues, but not excluding such features as the slope and texture of the ground and the broad facts of light and shade.

Rabaud says that "the return to the nest in no way leads us to assume any unknown sense which would merit the name of sense of orientation". He is willing, however, to admit a muscular memory or enregistration of movements. In many cases ants lose their way badly, but against that has to be placed their frequent short-cuts home. Without hesitation they will often cut across the hypotenuse of a triangle whose two other sides they described on their outward journey.

A bee carried from the hive in a box and liberated at a distance of a mile will often rise in the air, circle round a little, and then make a bee-line for home. This seems almost magical, but very careful experiments have made it practically certain that bees build up a general visual impression of their district. "The cues are relations between objects rather than the objects themselves", as is illustrated by their behaviour when the hive is shifted a little during their absence. They persist in going to the place where the hive should have been.

Within a short distance, the smell of the hive seems to afford a sure clue of a different kind; but the chief clue is visual. Yet the remarkable recent experiments of Wolf suggest that there is more than Rabaud is inclined to allow. Bees were fed at a spot 150 yards north of the hive. Even after short imprisonment in a box none of these bees had any difficulty in flying straight home. But if one was boxed and carried to a spot 150 yards east of the hive and there liberated, it flew 150 yards south and then began to hesitate. After hesitation and circling it proceeded to find its way home by the tentative method of visual search. If carried a couple of miles on to a lake, bees do not "home"; for there are no landmarks on the water.

The theory of learning the way that applies to ants and bees does not as yet work well in reference to migratory birds. For in many cases the young birds set off by themselves, to all appearance, on their long journey to an unknown goal.

In the case of the cuckoo, the parent birds leave their progeny behind them to make the long southward journey alone, unless indeed they sometimes get help from their foster-parents. In many birds, moreover, the return route in spring is different from that which is followed in autumn. In a number of cases it has been proved that the young bird, after wintering in the south, returns in spring to the precise place of its birth.

The migration itself is an hereditarily established racial custom; and while the way-finding may be in part a response to visual and other stimuli, it is very difficult at present to avoid the conclusion that there is an hereditary memory of the general direction to be followed in the autumnal and vernal flights.

Rabaud is against the postulate of a special sense; but it remains

very difficult to understand how a percentage of terns can find their way back to their nests when transported in closed baskets to unknown waters outside their migrational range, and from a distance of 800 miles. It is possible that a much-needed clue to homing in higher animals might be obtained by the patient and sceptical study of the orientating achievements exhibited by cats and dogs, and some other mammals.

At present it seems probable that homing in lower animals is the outcome of experience, while that of higher animals depends on innate endowment. Thus it is interesting to recall the fact that when the queen humble-bee has found a suitable nesting-place, she is careful to take her bearings so that she can find her way back after a flight. Here we may quote an instructive passage from Mr. F. W. L. Sladen's *Humble Bee.* "The queen crawls round the entrance, and poises herself towards it as she takes wing. Then she rises slowly, and taking careful notice of all the surroundings, describes a series of circles, each one larger and swifter than the last. So doing she disappears, but soon she returns and without much difficulty rediscovers the entrance. Similar but less elaborate evolutions are made at the second and third departures from the nest, and soon her lesson has been learnt so well that her coming and going are straight and swift." We cite this passage from an experienced observer because it suggests that the homing power in insects is different from that in birds and mammals. Terns, as we have mentioned, will return from their liberation in unknown seas hundreds of miles away. A cat, taken by train from Fife to Ayrshire, has found its way home. In such cases—and they are typical—there is no question of mastering the topography.

Some data for horses have been recently forthcoming. A two-year-old horse taken to a new place at some distance late in the evening, in part in darkness, found its way home next morning. It seems that a horse can find its way home in wild Australian country from a distance of 50 miles. There is abundant evidence that in thick darkness or in fog some horses may be trusted to find their way home. Sometimes they have proved to be right when their master thought they were quite wrong. In estimating the data there should be in the first instance a ruling out of all cases of habituation, for this complicates the issue. Moreover, every rider and driver knows that horses have a keen topographical memory. They register difficulties and peculiarities of a road, even when their experience of it is very slender. The most interesting data relate to homing from a new place at a considerable distance, and it would be interesting to find out how many tentatives or even mistakes the clever creature makes. It would be of great interest to make the crucial experiment of transporting the animal in a horse-box during the night, and then observing if it made for home.

BIOLOGY OF THE TONGUE.—It is an ambitious task for the tongue to tell the story of its own evolution. For there must have been an evolution, since the first tongues (in fishes) were non-mobile, and there were many millions of years before there was any tongue at all. We must not, of course, mix up the tongue with the vocal cords, which are the voice-producing structures, but as the tongue has often had its share in modifying sounds, it is not irrelevant to think for a moment of the ages in which there was no sound of life upon the earth. There were cosmic sounds of wind and wave, of thunder and cataract, but no voice of life. The age-long silence, as far as living creatures were concerned, was probably first broken by the instrumental sounds of insects like crickets and grasshoppers, produced by rubbing one part of the body against the other; but the first true voice was in all likelihood that of pioneer Amphibians that emerged towards the end of the Old Red Sandstone Age. Nowadays, at any rate, Amphibians are the lowest animals to show vocal cords and to utter controlled sounds, and it is interesting to note that they are also the first animals to show a movable tongue.

Many fishes have a tongue, and it is easy to see a cod's in the fishmonger's window; but the tongue in fishes is non-mobile, without intrinsic muscles. The so-called "tongue" of lampreys and hags, which is used to work the boring apparatus and is very muscular, must be excluded from the series, for it is not homologous with other tongues. In fishes the tongue is a sensory organ, for touch and taste, and in some cases, since it bears teeth, it probably serves to grip the food before swallowing. Of course it can be moved as a whole when the floor of the mouth is raised, but it cannot move of itself, so to speak.

Almost the same state of affairs is seen in some of the newts, where the tongue cannot be moved; and in some other Amphibians, like the Surinam Toad and the Clawed Toads, the tongue is absent altogether. We turn to the common frog, however, and we find a tongue very highly developed. It is fixed in front and loose behind, the very opposite of our own, and being well provided with intrinsic muscles it can be jerked out to a considerable distance on an unsuspecting insect. Moreover, a large glandular region, that the fish does not show, has been differentiated, and this produces a sticky secretion very useful in insect-catching. The frog's tongue is folded back on the floor of the mouth and has a broad, slightly forked, free end, which is farthest in when at rest, but farthest out when the catapult has been discharged. A very interesting little point is that the tongue of the tadpole is at first so slightly muscular that it cannot move itself. It is believed, however, that the included muscle-fibres are of some primary service in compressing the tongue-glands. Gradually they become stronger and able to move the young frog's tongue. Thus individual development recapitulates racial evolution.

Among reptiles the tongue is oftenest a touch and taste organ, but it sometimes helps in catching the booty. The masterpiece is the chameleon's, which may be seven inches in length—as long as the body without counting the tail. A dead specimen with the tongue out and the tail dangling looks as if it had a tail at both ends, like the Irishman's elephant. The chameleon focuses first one eye and then the other and, having reached with imperceptibly slow movements the striking distance, it projects its tongue like a lasso. The clubbed end is very sticky, and in a flash the moth is in the reptile's mouth.

It is interesting to watch a snake's tongue quickly and tremulously passing out from the mouth and in again. It ends typically in two delicate filaments. As in most lizards, its use is for touch and taste, and it has nothing to do with the poison, which is squeezed out along the groove on or actually within the fang-like teeth. Snakes use their tongue in feeling their way and in testing their food, but not in salivating their prey as used to be believed. In crocodiles and turtles the tongue lies flat on the floor of the mouth, and is not protrusible.

Among birds the tongue suddenly attains to great plasticity of form; in nearly related types it may be very different, apparently in relation to the fact that the food is very varied. Thus in those woodpeckers that feed mainly on sap, the tip of the comparatively short tongue is beset with numerous hair-like processes forming a kind of brush, and the sweet fluid ascends in the capillary spaces between. But in those woodpeckers that are insectivorous the tongue ends in spines, not in a brush, and the length is extraordinary. In the common American "Flicker" the tongue can be shot out for two or three inches beyond the tip of the beak, and it is connected at the back of the mouth with two long, curved branches of bone (the hyoid), which are continued upwards over the occiput of the skull and then forwards into the right nostril! "So when this bird stretches out its tongue the tips of the rear branches leave the opening of the nose, and shoot around over the surface of the skull until they have gone as far as possible." Even the burrowing ants have not much chance when the woodpecker begins to "flick" with its long, slender white tongue. Yet it is interesting to notice that in most, if not all, birds the intrinsic muscles of the tongue have disappeared. The organ is worked by muscles outside itself.

What contrasts there are: for instance, between the thread-like tongue of the humming-bird, more or less split and frayed near the tip, and the thick, fleshy tongue of the flamingo, deeply sunk in the lower jaw and bordered with soft, tooth-shaped processes. The toucan has a long, thin tongue, fringed like a feather; the cockatoo's is like a fleshy club; the duck's is broad and intricately fringed in

adaptation to mud-sifting; the pelican, with its huge gape, has a small tongue like a toothpick.

In mammals the tongue has its own muscles, and besides being a taste-organ, it often plays an important part in securing the food. It has been made the subject of an elaborate monograph by the late Dr. Charles Sonntag, anatomist to the Zoological Society of London. The tongue fills the mouth in all mammals except in the duckmole, some rodents, and some of the adult toothed whales, where it lies far back. In ant-eaters it is worm-like and mobile, copiously covered with glutinous secretion, so that it forms a very effective insect-catching instrument. The giraffe has a prehensile tongue, useful in drawing leaves into the mouth, and some bats have a tongue suited for probing into night-blooming flowers in search of insects. Everyone is familiar with the rough papillæ on a cat's tongue, which make it feel like sandpaper when puss licks our finger. These strong papillæ are characteristic of the feline carnivores, and are usually interpreted as adapted for rasping remnants of flesh from off the bones. But it is very probable that at least part of their significance is in connection with the toilet, for the tongue serves the fur as sponge and brush in one. Another use of the tongue is many mammals is in lapping up water, as we see so well in the dog. Apart from assistance in voice-production and discrimination of food by taste, one of the highest uses of the tongue is in exploring a crevice where something edible may be expected, or in testing the texture and amenities of the food. In some of the half-monkeys, such as Lemur itself, the tongue tests the food very carefully before it is taken into the mouth; and, as Dr. Sonntag wrote: "It must not be forgotten that the human infant gains information of its environment by touching objects with the point of its tongue."

ANIMAL HYPNOSIS.—One of the oldest of biological tricks was that played by the magicians before Pharaoh when they cast down every man his rod, and the rods became serpents. For, according to the higher criticism, the rods were snakes in a rigid hypnotic state. What Aaron's rod was is another question, for it swallowed all the others. Prof. Verworn tells us in his *General Physiology* that "by slight pressure in the neck-region it is possible to make a wildly excited, hissing, upstanding hooded cobra suddenly motionless, so that the dangerous creature can be put into any desired position without fear of its fatal bite". For various reasons we have not tried this particular experiment, but we have verified some others, as with the frog; and the state into which the animal passes is very puzzling. One excitation is antagonised by another, and the creature reacts to the physiological contradiction in terms by becoming stiff and stark. We shall improve on this statement later on.

The great French naturalist, Henri Fabre, confesses that as a schoolboy he used to combine with other spirits like himself in hypnotising the unpopular neighbour's guinea-fowl. They were brought into the strange, stiff state and then laid in a row along the top of a wall. By and by, of course, they came all right again, just as in the case of the magician's rod-like snakes. The boys were repeating the ancient experiment of making hens motionless, a trick which Father Kircher described in detail long ago (1646), as "experimentum mirabile de imaginatione gallinæ", for it was not then out of the fashion to credit a hen with imagination!

Animal hypnosis is different from the common hypnotic state in man, but it is an analogous phenomenon, and it can be induced in a large number of widely separated types: in guinea-pigs and rabbits, and even in cats, in fowls and pigeons, in snakes and lizards, in frogs and fishes, in crabs and crayfishes, and in many insects. The fisher-boys play with small "partans", holding them between finger and thumb, and swinging them two or three times backwards and forwards in the air, the result being that the crabs pass into the state of animal hypnosis. Similarly, if we stand the freshwater crayfish head downwards on the table, using the broadened-out forceps for pedestal, and gently but firmly prevent the tail from flapping, the animal becomes stiff and irresponsive, and remains in this strange inverted position for many minutes. If the forceps are properly arranged, so that the creature will be physically stable when our hand is removed, very quaint attitudes become possible; the crayfish may look like a leaning tower of Pisa—only upside down, and with a crutch!

Sometimes a sudden change is enough to bring about the immobility, the stiff cramp as we may call it. Thus it is often enough to transfer a brittle-star very quickly from the aquarium to a dry table, to see it assume the stiff cramp state, so stiff that one can lift the whole animal horizontally by the last inch of one of its normally very brittle arms.

Many years ago at a meeting of a physiological society we saw a woman who became hypnotic and stood rigidly when she shut her eyes. The stream of impressions entering by the eyes was needed to keep the body awake, just as if the inmates of a house fell asleep if people did not keep knocking at the door. So it has been suggested that the sudden lifting of an animal off the ground or out of the water may break the stimulating circuit that keeps the body from sinking into hypnosis. Sometimes it is enough to keep the animal, like the little aquatic worm Pristina, from touching anything rough. Even a few grains of sand will serve to keep it going.

This is of particular interest, because sudden changes, such as dislodgments, may be of frequent occurrence in certain natural conditions, such as the rough-and-tumble life of the seashore or

the wind-shaken environment of the herbage. A reflex that brings about immobility may be very profitable in such circumstances, for when an animal keeps perfectly still it is less likely to be pounced upon by enemies, many of which will not look at booty that does not move. And although among higher animals there is an interesting automatic adjustment of the falling body, so that it "falls on its feet", it is probably on the whole advantageous not to be very energetic when there is an accident.

Many insects, like the black dung-beetle, the death-watch, the ant-lion larva, and the stick-insects, show a ready assumption of the cataleptic or "death-feigning" immobility, which is at any rate closely analogous to animal hypnosis. It is enough to take the water-bug Ranatra brusquely out of the pond to see it become as stiff as a dry twig. A fall, a good shaking (as in children!), a slight pressure, a nip, a sudden blaze of light, and so on, may serve to induce cramp-immobility. Many experiments have been made with the common stick-insect (*Dixippus morosus*), which moves cautiously about at night, but remains motionless and twig-like by day. By letting the quaint creature fall twice or thrice, and in other ways, it is easy to induce the so-called cataleptic state; and the way in which the arms of a human cataleptic can be bent and fixed in a peculiar position is readily mimicked in Dixippus. The insect will remain standing on its head for an hour, yet it is enough to breathe on the creature to bring it back to normal life. It may be mentioned that the cataleptic state in this type is not assumed unless the brain is quite uninjured. The stick-insect is so immobile in its catalepsy that it can be stretched like a bridge between two books lying on the table; and then it may even be weighted in the middle with paper-clips! We believe that this insect holds the record for the duration of its immobility, which may last for four and a half hours.

There are doubtless different grades of animal hypnosis; thus there must be a long inclined plane between a hypnosed suckling pig that cannot move, yet follows us about with its eyes, and the catalepsy of a stick-insect, or between the death-feigning of a spider and the "stiff-cramp" of a brittle-star. What is common to all cases is, first of all, some abrupt change that "shocks" the nervous system, and sometimes prevents the normal answer being given to an excitation. This may be followed, in experimental cases at least, by an increased intensity of muscular effort, which is not allowed to become effective. In the second place, whether the phase of intensified effort be passed through or not, there is a marked change in the normal tonus of the muscles. When muscles are not being contracted in the ordinary way, associated with moving about or doing external or internal work, they are in a state of tonus. This means, if we may treat a difficult subject lightly, that they are in a state of slight permanent contraction, in obedience

to persistent gentle stimuli from the central nervous system. In this state there is no increase of chemical expenditure, as there is in ordinary contraction, and there is no fatigue. Now in animal hypnosis there is a marked change in this tonus, either an increase of its intensity (hypertonic), as in Arthropods, or a decrease of its intensity (hypotonic), as in most hypnotisable vertebrates.

Some day it will be possible to make a scientific inclined plane including the psychical hypnosis in man (and probably in a few mammals), the various grades of artificial and natural animal hypnosis, both hypotonic and hypertonic, till we touch bottom in the shock cramp of very simple creatures like brittle-stars. We have probably to do with a reflex that has been repeatedly seized upon and made of great service in life-preserving—sometimes even in life-continuance.

NATURE OF SLEEP

Except to habitual dreamers, sleep is a practically uninteresting state, a blank *dies non*, that recurs over a large fraction—about a third—of our life! One grudges the time one spends in sleep, and it is one of the consolations of ageing that for a long time we require less sleep. Yet we should not like to be guinea-pigs, which are said not to sleep at all.

But while sleep is practically uninteresting, it is very different when we think of it theoretically. It is a brain-stretching problem, full of psycho-biological interest. Thus the number of theories about sleep is huge. One recalls the crowd of theories in regard to sex, another everyday phenomenon whose true inwardness is still unknown or uncertain.

The problem need not be complicated by using the word "sleep" in a loose way. Thus hibernation is certainly not sleep, nor is coma, nor trance. The "sleep" of plants is a misnomer, and while we may have our opinions, we have no certainty as to the occurrence of true sleep below the level of mammals and birds. True sleep is part of an established rhythm, and implies a state of partial fatigue and rest in the higher nerve-centres, during which recuperation occurs, perhaps in part associated with the removal of inhibiting waste-products or toxins. Yet it is certain that our whole nervous system does not fall asleep, for the "breathing centre" in our medulla must be always awake; and so is it with many parts of the body, such as heart, kidneys, and alimentary canal, which require some nervous control. Even our muscles are not quite inactive when we are sleeping, else we should soon become cold, even under a quilt.

Familiarly wrapped up with sleep are several subsidiary features, not quite essential. Thus by closing our eyes and shutting out light

and noise, we get rid of many of the knocks at the door of our awareness; we are unable to answer the door with our usual promptitude; and we cannot normally move about without awakening. There is some somnolence, so to speak, throughout the body, for the pulse and breathing are slower and the temperature sinks a little. The mental aspect of life is very inconspicuous in deep sleep? at least we infer this from so often remembering nothing of our dreams.

Yet a difficulty is raised by the fact that the rest characteristic of sleep is so *partial*. Although the heart gets a little rest between each beat, it is not easy to understand its persistent, normally tireless, activity. Why should it not need the relative rest which most muscular tissues seem to require, which they find in sleep? Much of the brain goes out of gear in sleep, but how is it that certain centres never cease to be active? What is this sleep that affects some parts so profoundly, and others so lightly?

In his recent admirable book on *Sleep and Its Disorders* (1929), Dr. R. D. Gillespie punctures one theory after another with gleeful adroitness. There is next to nothing in the view that sleep is induced by the circulation through the brain becoming slowed down, because the blood has become more viscous, because the hard-worked nerve-cells have used up so much water. Beautiful but almost baseless is the theory of Duval, that the branches of adjacent nerve-cells cease at bedtime to be in contact, so that neural circuits are broken. Very attractive is the theory of Piéron and others that prolonged loss of sleep produces a poisonous "hypnotoxin" which compels sleep by inhibiting activity in nerve-cells. But how often we cannot sleep when we are very tired, how often we sleep soundly when we are not tired at all, how often people fall asleep without apparent cause. Moreover, we have first to catch our hypnotoxin. Of course, the inducing of sleep has been referred to the regulatory rôle of the hormone-making glands; but these have already a very heavy burden to bear.

The favourite theory at present is that the brain includes a special sleep-governing centre, situated, according to some, in the central grey matter; according to others, in the region called the thalamus. Just as there is a temperature-regulating or thermotaxic centre (in the *corpus striatum* of the fore-brain), so there is considerable evidence of the existence of a nerve-centre that regulates the complex function and abeyance of function which we call "sleep". By an ingenious combination of studies on sleeplessness and other disorders, on soporifics, and on the labyrinthine structure of the brain, it has been possible to make out a fair case for the theory that ionic changes in a centre in the floor of the thalamus bring about sleeping and waking again. Changes in calcium-ion concentration in the blood influence the permeability of cell membrancs, which

affects electrical conductivity between each side of the membrane; and there seems to be an increase in the electrical resistance of the body generally during sleep. This, at any rate, is a vigorous theory of to-day, that a centre in the floor of the brain is the seat of physiological processes which initiate, maintain, and abolish sleep.

But this theory, as Dr. Gillespie shows, can be made more circumstantial. Pavlov and others have proved that prolonged stimulation, followed by responses, may bring about in the implicated nerve-cells an inhibitory state which prevents further activity for the time being. This has a protective value, for it prevents excessive fatigue of the brain. Now it may be that sleep is due to an irradiation of inhibitory influences from a focus gradually evolved for that function, and situated apparently in the thalamic region of the brain. The irradiation of the inhibitory commands may be brought about by over-stimulation and consequent fatigue, but also by a shutting out of stimuli; and account must also be taken of established rhythms and habituations. For all these problems there are two approaches—the physiological and the psychological. The former leads us to think of changes in the calcium metabolism, in the permeability of cell membranes, in electric potential, and so forth. The other leads us to think of a safeguard that prevents the restless mind from overtiring the weak flesh. Sleep is a tax on keen wits. And that, dear reader, is why you are so often sleepy! The more wideawake you are, intellectually and artistically, the more sleep you require. There is a warning to man in the guinea-pig that does not sleep!

Sleeplessness.—It is very doubtful if true sleep ever occurs except in warm-blooded animals (birds and mammals), and it does not seem to occur in all of these. Sleep is an established bodily habit or rhythm, which brings about a quieting down of activities, and, as we have said, it is probably regulated automatically by a special centre in the brain, just like the heat-regulating centre which keeps the temperature of our body practically constant, day and night. Sleep puts on a brake over the whole body; it inhibits the usual answers-back to stimuli; it shuts the doors and draws down the blinds; it acts as a safeguard against the fatigue-collapse which is apt to follow the often-repeated response to the same kind of excitement. A certain amount of fatigue may be useful in prompting the sleep centre to exert its beneficent life-saving influence in enforcing rest, but the favourite theory that sleep is a self-intoxication of the body and brain with the fatigue-toxins of prolonged activity is far too simple. Many people know what it is to be too tired to sleep; many sleep very soundly who never know what it is to be tired.

While it seems wisest to regard the true inwardness of sleep as still a problem, if not a puzzle, we know a good deal about its

normal concomitants. There is a general diminution of activity, as seen in the slowed pulse, breathing movements, and chemical routine or metabolism. There is also a reduction in food-canal movements and in almost all activities except perspiration. There is delay at the thresholds of the sense-organs and of the nerve-centres; and consciousness is often switched off, so to speak. One must try to distinguish concomitants of sleep from changes associated with resting (e.g. lowered temperature), or with lying flat (e.g. increased blood-pressure in the brain).

In his recent masterly book on sleep, Dr. R. D. Gillespie does good service in puncturing the prevalent exaggeration of the danger of insomnia in man. It has often been said that a dog will die of sleeplessness sooner than of starvation, and there is indubitable evidence that enforced wakefulness may be fatal to an intelligent animal. But there is not much evidence that prolonged sleeplessness has either mental or bodily ill-effects in man. In a few cases there has been a delirium, but after a good sleep the patient was all right again. Those who are sleeping very badly should recognise that this is a danger-signal pointing to something that urgently requires attention, but they should not brood over the idea that the sleeplessness itself means a collapse. There are few well-documented cases of very profound insomnia continued for many days and nights; and room-mates of those who say in the morning that they "never slept a wink" have often a different story to tell!

Some disorders of sleep are so serious that a physician's counsel should be sought for without delay. We refer to cases where the difficulty of falling asleep is so prolonged and irksome that the prospect of bedtime is almost a terror; to cases where people sleep too much, not too little, or when they fall asleep at the wrong time and in awkward situations; to cases of habitual nightmare, recurrent night-terror, frequent somnambulism, and so forth. These indicate something in the way of brain disturbances, or something going wrong in the body which puts the sleep centre out of gear.

But quite apart from serious disorders, there is frequent failure to get a good night's rest, and this is often a quite unnecessary handicapping of daily vigour.

We refer to cases where the "bad sleeper" tosses about "for hours" before he becomes somnolent, or wakes up at frequent intervals, or is pursued by bad dreams which may end in a convulsive start or in profuse perspiration, or is given to talking in his sleep, or rouses himself with difficulty and unrefreshed when the alarum-clock sounds in the morning. Or sometimes it is merely that the sleep is not sound enough, but is broken by trivial noises, or seems to the bad sleeper to be continually invaded by a wearisome repetition of often-repeated daily tasks and worries. Are there any

general principles which may guide reasonable people to spend a third of their life a little more pleasantly and profitably?

"Sleeping badly" is like pain, for it is a danger-signal that all is not well with the body; and the first problem is to find out what is wrong. The answer is often humdrum—too much digestion and indigestion after too late a meal; too little honest work to induce a reasonable amount of fatigue; too great a strain on the liver and the kidneys, which have to do with getting rid of the nitrogenous waste of the body; in rarer cases over-fatigue; in some cases actual pain, as in toothache and earache. To cure this minor "sleeping badly", one must remove its cause, and that, though seldom easy, is in most cases possible.

Remediable also in some measure are the environmental artificialities and disturbances which so often knock at the doors of the senses before these have been barred by deep sleep. Sound sleep asks for quiet and for darkness, as well as for a decently healthy body. Yet one must not make a scapegoat of the environment, for there is a terrible truth in the saying: "One hears only the noises one listens for."

Bergson says somewhere that we will not fall asleep if we continue more interested in something else than in enjoying a rest. That something else may be an intellectual problem, a hydra-headed practical anxiety, a great task ahead, a deep sorrow, a dread, an obsession, and so on through a long and familiar list. What we must do is to allow the brain a chance to give the mind a holiday for the night; but, until the doctor tells us, that holiday of sleep should not be secured by any dope. It is good business to think over next day's duties, but it is bad business to do that in bed; it is good for us to have an intellectual problem to chew at, but we should not start our mastication when we wish to sleep. All devices like counting sheep are contradictions in terms; the only profitable relaxation after our head touches the pillow is bodily relaxation, and perhaps an easygoing recollection of pleasant pictures from the past. Best of all to be as the babe in Mother's arms: hence the old phrase "in the arms of Morpheus".

THE PHYSIOLOGY OF AWAKENING.—Given sleep, how comes waking? With the conclusion of the repair and renewal process, no doubt; yet how is the actual awakening accomplished? In many cases simply; as fundamentally by the needs of eliminating waste-products—for in simple and rural civilisations, such as that of India perhaps especially, this is a first care, a practically universal habit, and of course the healthiest possible. Among the manifold confusions and inhibitions of our urbanised civilisation the clearing of bowel-waste is apt to be delayed, as so often, till after the first meal, if not even longer; but in all cases the more imperative need

of relieving bladder-strain appears to afford a main stimulus to arousal; indeed, physiologists have traced the steps of the process in due detail. Again, that organic time-sense, often so clear in ourselves, and dawning in our domestic animals at least, by which we can suggest to ourselves overnight even a very early waking without help of an alarum-clock, no doubt also plays its part, as indeed every day in habitually ordered life, on which regular sleep and active life alike so much depend, and health and long life accordingly. In fact, is not longevity very largely, if not mainly, the reward of such well-acquired habits, with that regular succession of good nights and good days which it is the fundamental essence of personal hygiene and self-education to acquire, as of all education worth the name to train into? When we again learn to think of life concretely as of old, in terms of days instead of years, we shall thus have more of each, and better also.

The Psychology of Awakening.—Yet we need to go farther; for sleep is more than mere neural and cerebral repose, no mere arrest of consciousness, but frequently—and to many normally—a period of renewal of the mental life no less than a freshening of the organic. For the latter, are not the active katabolisms of the previous day made up for, and often richly, by the anabolic process of the night?—for not merely do children grow during sleep, but the adult stature is restored as well; so that a recruit just below the limit of acceptance in the afternoon or evening may reach it when measured next morning (as indeed the story goes of the late Lord Roberts). At any cheerful breakfast-table, each notices how many of the circle are "looking well", i.e. better than they did the night before; and are they not often mentally brighter also? And this not simply by removal and repair of the previous day's tear and wear, but by a real advance beyond its depressing difficulties, which can now be faced anew and often more readily overcome. "La nuit porte conseil" is a very common French saying; and it plainly corresponds to "sleep over it" in English. The psalmist's line—translated in the Authorised Version as "He giveth his beloved sleep"—has been revised and extended into the yet fuller saying and richer promise—"He giveth to His beloved in sleep"—on which we have heard, in an at first expectation unpromising little country church, an admirable psychologist's sermon. Too many, no doubt, may say they lack this happy and fruitful experience; yet not a few of these, when questioned, can remember how in school-days the solution of the problem one had failed to puzzle out overnight was simply there next morning on awakening and standing out clear, without any conscious reflection at all. Here even is an extenuation of the law's delays; for what better help for the tired judge—after conflicting evidence and contradictory partial pleadings, to each of which he has given fair-minded hearing, and reflec-

tion too, consultation of legal and perhaps other authorities as well —than a good night's sleep, a clear week-end, perhaps even a whole vacation! A sudden solution may, of course, come at other times: one says and hears "It strikes me!" at any hour of day; yet surely for most normally living and thinking people oftenest in the morning. Normal sleeping, too, seems needed, and that is (at any rate seems) dreamless; for while admitting that dreams too are sometimes helpful, we incline to think of such as but pre-waking forecasts towards the solutions; and of the more ordinary dreams, despite Freud's marvellous interpretations of so many of them, as overmingled with vaguer thought-wanderings, such as we all know in moods of reverie and moments of phantasy even by day, and which so largely pass and are forgotten, as they mostly deserve, since unadapted to our real activities of life. No doubt the poet and the artist make more of these than do the rest of us; yet does not the great rise of dream-interpretation with Freud and his disciples go in the main to indicate the abnormality of such conscious dreaming; for is it not just their distressed patients that they have first and best interpreted? And though they have come also to contribute interpretations, and these often acute, of those higher dreamers to whom the world's progress has been so largely due, are they not still more or less biased by their pathological approach? For is not the safer approach the developmental one, that of beginning with the normal and happy sleep of infancy and childhood?

Starting here, and listening to one of the most sympathetic—and thus wisest—of educationalists, Margaret McMillan, to our mind on lines even surpassing those of Montessori, we have heard her discourse on her ideal training college for teachers. In this her many counsels of perfection culminated in selecting the very finest of all her applied psychologists to what she claimed as the most important of all educational tasks—that of putting the children to sleep—thus happily inspired! And must not those of us who have had such vital experience through childhood agree with her? Do we not here find the mother-instinct at its best as well as simplest, and even fatherly wisdom too?

Is it objected that most students prefer to study late rather than early? Yes; but two fresh considerations here arise: first, that human life, throughout its rise, its pre-history, and history up to the present, is far more spent in activities than in thought, and that the brain—of youth especially—is thus above all concerned with the direction of individual movements, far more than with the interpretation of other and more general ones. So it is but natural that it should have its main day's work well over (though not to positive fatigue) before settling down to face at all, or, still more seriously, share the recorded activities of maturer minds. Secondly,

such facing, for most, is mainly of understanding and remembering, with at first but little of serious sharing. But when that—in what are still too few cases—once clearly begins, are not the waking moments, the early hours, of most value? Despite all the difficulties which social life tends to impose, is there not much evidence for this in the biographies of the past, and even among the productive lives of our surely peculiarly difficult present? Let whoever doubts this submit the matter to fair experiment—difficult, of course, since involving the change from preponderance of nocturnal acquisition to that of waking and morning thought-habits. For, like the man who first said, "Honesty is the best policy", and who, when asked how he discovered this, answered, "I've tried both!" so in this present matter can we, and so before long may he. It is, at any rate, well worth trying.

Some of the really good "coaches"—who so often teach better, because more psychologically, than do we professors, apt to be too intent upon our subject merely—have among their devices that of exercising their pupils in given subjects at the hour fixed for the coming examination; so as to form the habit beforehand of thinking mathematically, or linguistically, or otherwise technically, at the given time of day; and this is naturally found "to pay". The matinal habit above pled for is surely no less deserving of fair experiment; indeed, far more, since aimed towards the free and full encouragement of each and all the individual's latent powers, and even to the habitualising of these towards their increasing development—so at once encouraging each latent aptitude in its needed growth, and backing it with that steadiness of habit which brings also the patience, so needed even for genius.

With the nowadays customary notion of "the rarity of genius" we have no patience. The "average man", "the average boy", "girl", and so on, is but a modern myth, of pedantised routine, and this now so much bureaucratised and industrialised, mechanised and mammonised as well. For as not only every human face is unique, but even thumb-mark as well, so with every mind. The best teachers are now beginning to know the literal truth of de Vigny's verse, and even to warn against its tragic close—

> Il existe en effet, chez les trois quarts des hommes,
> Un poète—mort jeune, à qui l'homme survit.

And again—

> Qu'est-ce que c'est qu'une grandevie? C'est une pensée de la jeunesse, executée dans l'âge mur.

So now that our long prevalent mis-instruction, with its obsession of "the three R's" as the one gateway of knowledge, is giving way

to the incipient Re-Education, with its three H's—Heart, Hand, and Head, for which the three R's are then so much more easily and soundly acquired, swiftly too, even by "explosion" as Montessori rightly calls it—there is good hope of coming increase of individual and social "efficiency", even to "genius". "Taylorian efficiency"—which as we now know beyond dispute can not only double or quadruple, but even sometimes septuple, the muscular abilities of labour—can thus be rivalled, and even surpassed, upon the more fully psychic and psych-organic levels. So if any reader doubt this, and with sufficient scientific openness and energetic patience for the needed experimental trials, let him join us in such endeavour.

SUSPENDED ANIMATION.—This old-fashioned term "suspended animation" is useful in its elasticity, for it is less precise than hibernation, lethargy, latent life, coma, animal hypnosis, catalepsy, and the like, and can be applied to a greater variety of cases. The hedgehogs are hibernators; the slow-worms lie torpid in the recesses of a mossy bank; the frogs huddle stiffly in a disused drain-pipe; the snails, with the mouth of the shell well sealed, hide in a deep corner of an old wall; the young queen humble-bee drowses through the cold months in some safe retreat underground; and so is it in winter for hundreds of other animals, not to speak of the seeds of plants which are lying dormant in the earth.

There is a long gamut between the hibernating bat and the desiccated, but certainly not dead, bear-animalcule or Tardigrade, but they have the common negative feature of suspended animation, to a greater or less extent. Some day it will be possible to arrange them in series; but that is not possible at present. What is certain is that we have to deal with several distinct sets of phenomena; thus the dormancy of a dried-up water-flea, which may survive for several years, is very different physiologically from the cataleptic inertness of a walking-stick insect; and both are very different from the sound sleep of a dog or a child, during which most of the bodily functions are continued vigorously. The winter-sleep of a bat is not like the dog's sleep, nor like the queen wasp's hibernal coma.

To the chemist, as we have seen, living implies the frequent upbuilding and downbreaking of carbon-compounds in a colloid state, and most characteristic of all is the metabolism of the proteins that form an essential part of the physical basis of life in all animals. This changefulness of proteins cannot continue except between somewhat narrow limits of temperature. It requires the presence of a large percentage of water along with the protoplasm. But an enormous reduction of the percentage of water, or of mobile water, is not necessarily fatal; for while the metabolism comes to a standstill, it can be resumed after hours or days or years when suitable conditions return. Everyone is familiar with the dryness of

many of the seeds in the seedsman's shop, and a desiccated thread-worm may be so dry that it breaks when we touch it with a needle. Yet, when water is supplied, it becomes agile once more. It seems, then, that the groups of large molecules—proteins in particular—may entirely cease their reactions with one another and with the outside world, without this necessarily precluding the reassumption of active relations at a subsequent date. The fatal change begins when the protein molecules begin to disintegrate. Even here, however, there may be no more than local death; for fatal disintegration may occur in a part without any surrender of the whole citadel of life. In many animals, as in most plants, the dying away of parts is normal.

Let us summon the "seven sleepers" before us. First, from the gutters of houses, come the sluggish microscopic "bear-animalcules", with four pairs of clawed legs. Some of them, seen sideways, are quaintly like minute rhinoceroses. When they are dried up, they become like much-weathered grains of sand; and they may remain for years without any discernible vitality. But when they are once more supplied with water, they swell up again and crawl away, as plump as little sucking-pigs.

Second, from amid moist bog-moss come the beautiful "Wheel animalcules" or rotifers, which often show an astounding capacity for "suspended animation". Sometimes the entire animal survives the prolonged drought; sometimes the body succumbs, but the eggs live on. Two hundred years ago the keen-eyed Leeuwenhoek was delighted to observe that the "wheels" began to go round again after they had entirely stopped during a prolonged drought.

Third, from damp earth and decaying organic matter, there comes a large contingent of paste-eels, vinegar-eels, ear-cockle worms, and other Nematodes, some of which can survive desiccation or drying-up for as many as twenty years. In this and in some other cases the process of revivification takes a longer or shorter time according to the duration of the dried-up quiescence when "life" appeared to be absent altogether.

The fourth set of sleepers are among the jointed-footed animals, or arthropods, including notably the thousands of insects that pass the winter in a state of suspended animation as larvæ, or as pupæ, or as adults. They become benumbed, we say, but we do not satisfactorily understand what happens. Their muscles go out of gear, and not only is there an entire stoppage of movement, but a loss of irritability to all sorts of stimuli. With this arthropod contingent should be associated the numerous minute crustaceans, which may become as dry as dust and remain so for years without a loss of vitality. When an egg, an embryo, or a seed remains in a state of latent life in this way, the marvel is big enough, but it is enhanced when we have to do with an intricate adult creature possessed of a

full equipment of organs. The fifth contingent includes the snails and slugs that often spend the winter in holes and burrows, relapsing into a very dead-alive state. A well-known snail sleeper awoke after many years to find itself in a museum case and provided with a label. Those who are fond of snails should eat them in the autumn, when they have stored their body with reserves, which sustain them during the winter's fast.

The sixth contingent includes the cold-blooded lower vertebrates, such as fishes that sleep through the dry season buried in the earth, the frogs that may be frozen stiff without dying, many tortoises that bury themselves alive for the winter, and crocodiles that while away the summer's heat ensconced in the hard-baked mud. Our British adder is a familiar instance of a reptile that lies very low throughout the winter.

The last contingent of the "seven sleepers" is that of the true hibernators, like hedgehog and hamster, dormouse and bat. This is a contingent by itself, including only a few imperfectly warm-blooded mammals; and the state of hibernation is neither cold-coma nor sleep. It is an interesting question whether men may remain for a long time in a state of suspended animation. Some regard the evidence as conclusively proving the possibility of a prolonged trance in which there is no trace of a pulse or heart-movement, and no dimming of a mirror with breath. The prolonged suspended animation of Indian fakirs has often been described by travellers, and there have been a few careful studies. The data are very puzzling. One cannot cite the case of the Master of Ballantrae as evidence of the possibility of coming alive again after being buried for a week; but what can one make of the case of Colonel Townsend? "He could die or expire when he pleased, and yet, by an effort or somehow, he could come to life again!"

In watching the sower flinging his seed, one may well feel a sort of catch in the breath—of wonder; since at once sentimental and scientific is this sudden awareness of a life-mystery. The life of these potential plants—these seeds of common cereals—what a strange state it is in! Even their living matter, apart from husk and store, is hard and brittle. There is no sign of life (unless it be an electrical reaction); and yet the seeds are not dead. Paul Becquerel subjected naked seeds of lucerne, mustard, and wheat for three weeks to the temperature of liquid air; then for seventy-seven hours to that of liquid hydrogen (250° below zero F.); and then put them into a vacuum for a year. The protoplasm lost its characteristic colloidal condition. Yet many of the hardly used seeds germinated after all! What is this strange state of latent life, without water, without air, without gaseous exchanges, without colloid molecules in suspension in a liquid? For all the living matter we ordinarily know has its physical basis in fluid condition. How does the vital current flow

again, after being frozen far harder than glacial ice? Is living necessarily continuous, or can it stop, like a jarred watch, and begin again? Whoever puts the question rightly will be on the way to an answer.

The "Advance of Science" is a phrase often on our lips, but the persistence of error is seldom referred to, for we are optimists with ourselves. One of the hardy perennials is the belief in the revivification of "mummy" wheat, and we read the other day in one of our leading newspapers that a farmer in Bathurst (N.S.W.) had raised a vigorous seven-eared crop from grains which had lain embalmed in Egypt for over 4,000 years. No doubt there are seeds that may retain their vitality for fourscore years or more, but every carefully investigated case of the alleged germination of mummy wheat has broken down. In most cases it turns out that the alleged mummy wheat was faked. *True mummy wheat is always dead.*

THE QUEST OF FOOD

It is interesting and educative to make a list of all the many different solutions that animals have found for the bread-and-butter problem. Here is our latest attempt. (1) An animal may devour a plant, as the cow the grass. (2) An animal may eat what a plant has made without harming the plant, as a bee the nectar. (3) A green animal may feed like a plant, utilising the sun's rays in photosynthesis; and it may be (*a*) green in its own right, like the green Bell animalcule, or (*b*) green, because of partner algæ, like the green freshwater sponge. (4) An animal may feed on another living animal, as a tiger on an antelope. (5) An animal may feed on dead flesh, like a carrion beetle. (6) An animal may live on rotten organic matter, prepared for it by bacteria, as is the case with many threadworms or nematodes. (7) An animal may feed on organic debris, or crumbs, as the earthworms on parts of plants lying on the ground. (8) An animal may depend on microscopic animals and plants in the surrounding water, like so many plankton-eating creatures of the open sea. (9) An animal may thrive through its partnership with another animal, whether an internal symbiosis (as in 3 (*b*)) or an external partnership like that between certain hermit-crabs and certain sea-anemones. (10) An animal may be an external parasite, cleaning up the surface of its host's skin, as in the case of lice and some mites. (11) An animal may be an internal parasite, living (*a*) on the digested food in the alimentary canal of its host, e.g. tapeworm; or living (*b*) on the actual tissue of its host, e.g. liver-fluke on the blood of the sheep's liver. (12) An animal may be a predatory animal from within—surely not strictly to be called a parasite—like the ichneumon grubs devouring the caterpillar.

SOME STRANGE BACTERIA.—In further illustration of nutritive peculiarities it is interesting to refer to the strange life of some Bacteria. To show these in proper relief, a slight recapitulation is necessary.

All living matter is made up of complex compounds of carbon, and the energy of vital processes is derived from the chemical breaking-down of these complex substances into simpler ones. In nearly all cases this breaking-down is accompanied by an uptake of oxygen gas from the atmosphere, so that the final product is carbon dioxide. In the same way, a candle takes oxygen from the air and gives off carbon dioxide as it burns; but the complex substances of the candle are gradually used up; a burning candle has a short life. Animals, on the other hand, constantly replace the carbon compounds as they are consumed; the food materials taken into the body make good the loss. It follows that animals, and some simple plants, depend on a food supply of suitable carbon compounds; without this they starve and die. The green plants, on the contrary, are not dependent on a food supply of carbon compounds; they entrap the energy of the sunlight, and with this energy build complex substances from the simple carbon dioxide they draw from the air. In the dark, deprived of the energy of light-rays, they are unable to do this. This is all familiar ground.

There are a few strange bacteria which build up carbon dioxide into complex compounds, even in the dark. The energy required for the formation of the complex substances is drawn not from light but from chemical reactions of varied and peculiar types.

One of these Bacteria, Beggiatoa by name, lives in natural mineral waters which contain that evil-smelling gas, sulphuretted hydrogen. From this compound the Beggiatoa forms ordinary yellow sulphur, of which the living cells show abundant granules. The sulphur is then combined with oxygen from the air to form sulphuric acid. From these reactions the bacterium derives enough energy to build carbon dioxide into the complex substances of which its living matter is composed.

Other bacteria solve the same problem in analogous ways, but make use of different energy-yielding chemical reactions. Some combine oxygen with iron, and become so clogged with rusty particles that they block up water-pipes and give endless trouble to engineers. Some combine hydrogen with oxygen to form water, and derive much energy from this! A large and important group carry out various reactions with nitrogen and its compounds, and play an indispensable part in preventing soils from becoming exhausted and useless for plant growth. How clearly these many solutions to one problem illustrate the adaptability of living organisms!

VITAMINS

The little things of this world often count for much more than the large. The invisible microbe kills the giant by multiplying in his blood and producing poisons which may be fatal within a few hours. So it is in a beneficent way with two kinds of things that are not related to one another, though they both work in very minute quantities, namely vitamins and hormones. Vitamins, which are also called "accessory food-factors", are substances or qualities of substances that are present in small amounts in many kinds of natural food. If they are absent, then the food, though otherwise quite wholesome, loses much of its efficacy for promoting health and growth. Hormones are invisible chemical messengers that are formed by several ductless glands in the body, especially in backboned animals, and are distributed by the blood, regulating the various internal activities. If they are not formed in sufficient quantity there is disharmony or disease, and similarly if they are produced in over-abundance. They are the regulators of the life of the body, and of the health of the mind as well. Let us take the vitamins first.

When people or animals feed exclusively on polished rice, with the delicate rind removed, the strange disease called Beri-Beri sets in, or some disturbance of an allied nature. The conclusion that most physiologists draw from this common experience is that an important chemical substance of some sort has been lost by the removal of the outermost zone of the rice grain.

This conclusion is confirmed by the fact that the disease can be checked and health restored by replacing what was removed, that is to say by using unpolished rice. Or the same result may be reached by adding to the polished rice diet a small quantity of some other kind of food, which is therefore believed to contain what was missing. Various kinds of vitamins have been studied during recent years, but we do not yet know their chemical nature or how they work. No vitamin has yet been obtained in a state of indubitable purity, though some investigators have probably come very near this desirable isolation.

How did our forefathers do without vitamins? The obvious answer is that they got on well on the whole, *though not always*, because vitamins are present in the natural mixed food that sensible people usually eat if they get a chance. A deficiency of vitamins arises when the diet is too monotonous, or too artificial, or when the food is much broken up and only part of it used, or when some very essential kind of food, such as milk for young children, is not forthcoming. As to rice, which is the staple food of a large fraction of the world's population, the evil effects of the artificial treatment

of the grains began to be striking when the rice-eating districts of the East were invaded by milling machinery from the West.

When our sailor forefathers went a long voyage with salt beef and the like as the main part of their sustenance, they did *not* get on well without vitamins, for they became afflicted with the horrible disease of scurvy, which is due to the absence of one of these powerful "accessory food-factors". We have changed all that, and scurvy has gone by the board. Apart from the shortening of voyages from port to port and the increased possibilities of carrying varied food for the voyage, the "deficiency disease" of scurvy can be kept away by serving out lime-juice. Some such precaution is now compulsory. In old days no one understood scurvy, but it is interesting that sailors should have chewed the common "scurvy-grass", or it might be dulse and other seaweeds, when they reached a shore. It was as if they felt that they needed something of that sort, and it is possible that some of the queer vagaries of appetite among animals and among children may be unconscious gropings after needed vitamins, which are formed primarily and mainly in the tissues of green plants.

The precise rôle of the indispensable accessory foodstuffs is still uncertain, but we may think of two possibilities. (*a*) It is possible that vitamins are essential constituents of the living matter of protoplasm, just as proteins are, and that they cannot be built up in the animal body, but have to be borrowed, as it were, from plants, or from the milk of vegetarian animals, and so on. The sickly child becomes vigorous when it gets supplies of cod-liver oil. The cod ate the whelk, which ate the worm, which throve on the minute green organisms of the sea. In other words, vitamins may pass from one embodiment or incarnation to another, although the animals concerned in the chain may not be able to manufacture them for themselves.

(*b*) But another view is that vitamins owe their value to some tonic influence which they exert on the chemical routine (or metabolism) of the body. They may be stimulating rather than nutritive. They are not ferments, but their virtue may be in acting as "catalysts". This means, as is explained in another study, that they accelerate chemical reactions which would otherwise be too sluggish to be of much avail.

Vitamins were practically discovered about twenty years ago by Prof. Sir Frederick Gowland Hopkins, the distinguished biochemist of Cambridge, but many experts have shared in their investigation. Let us notice briefly the various kinds that have been distinguished. (A) The fat-soluble vitamin A, first detected in butter and yolk of egg, is abundant in cod-liver oil and in many vegetable oils. Its primary source is in green leaves and seaweeds. It seems to promote growth and to have something to do with the

utilisation of fat in the body and with resistance to infectious diseases.

(B) Water-soluble vitamin B is found in cereals, pulses, eggs, yeast ("marmite"), lemons, and the like. It counteracts beri-beri disease and works against certain forms of nervous breaking-down. It is technically called "anti-neuritic". It is now generally regarded as a complex of several vitamins.

(C) Vitamin C, which works against scurvy, is abundant in green vegetable like cress, in fresh fruits like lemons, and especially in sprouting seeds. It is technically called anti-scorbutic.

(D) Allied to fat-soluble vitamin A is another with similar physical properties and distribution, which works against imperfect bone-forming in children, in other words against "rickets". It is therefore technically called anti-rachitic. But its work in promoting the proper use of lime-salts in bone-making has to be backed up by plenty of sunlight.

(E) Of great interest, but clouded in uncertainty, is a new fat-soluble vitamin E, abundant in ether-extract of wheat embryos, and in dried leaves of lettuce. It occurs unhurt in dried leaves of peas, in seeds like cotton and Indian corn, in some fruits like bananas, in yolk of egg, and in many animal tissues. Experiments with rats indicate that this vitamin is necessary for the successful development and birth of offspring. Perhaps the biggest fact in regard to all these vitamins is simply that they are abundantly present in mixed natural food, not too much cooked, and not made over-dainty.

VITAMINS AND LIGHT.—It is now a widely-known fact that an adequate diet must contain not merely sufficient proteins, fats and carbohydrates to furnish energy and maintain the tissues of the body, but also, as above noted, certain "accessory food-factors" or "vitamins" essential to health. For example, an artificial milk can be made up, containing the same proteins, fats and carbohydrates as natural milk; but animals fed on such a synthetic diet cease to grow, develop various definite disorders, and presently die, in the absence of the vitamins which natural milks, and many other natural foods, contain. Inadequate supplies of certain of these vitamins lead, in man, to disorders like beri-beri and scurvy. Many natural fats (butter, cod-liver oil) contain vitamins in whose total or partial absence young animals cease to grow, fail to form bones correctly (rickets), and become subject to disorders of the breathing-passages on the one hand and of the eye (xerophthalmia) on the other. It is probable that at least two factors are missing or deficient in such cases; their chemical nature, it must be said, is quite unknown. It is found that exposure to sunlight helps animals, such as rats, to ward off the eye disorders due to a deficiency of "vitamin A" in the diet. Ultra-violet light, which,

though invisible to our eyes, is chemically active and affects the photographic plate, has a great influence in promoting growth and preventing rickets in rats whose diet is partly deficient in the necessary vitamin.

A very remarkable discovery recently made is that if rats kept on a deficient diet and not fortified by ultra-violet light are fed with the flesh of other rats which have been treated with the ultra-violet rays, they thrive and escape rickets. Still more remarkable is the discovery just announced by Steenbock and Black: that if the food-ration, known to be deficient in the rickets-preventing vitamin, is exposed to ultra-violet light before being fed to the rats, it mysteriously becomes adequate and sufficient. It seems that ultra-violet light can bring about formation of the vitamin from a known chemical substance, ergosterol, a complex solid alcohol widely distributed in plants and animals, but nowhere very abundant; but it is still too soon to jump to so definite a conclusion. Indeed, the discoverers are inclined to abandon the idea of a definite rickets-preventing substance, and to suppose that some form of radiant energy is the active agent. But it is difficult to picture this in terms of modern physics.

A Vitamin in Development.—On general grounds great caution should be exercised in naming new vitamins, which have not been isolated or chemically determined. For a vitamin is little more than a name for a hypothetical substance whose absence from the food is followed by certain evil results. But there has been some recent evidence of the existence of a new fat-soluble vitamin E, a substance necessary in the food-supply of the mother if the embryo is to complete its development. It has been called the vitamin of reproduction.

The new vitamin is abundant in the ether extract of wheat embryos and in dried leaves of lettuce. It occurs unhurt in the carefully desiccated leaves of alfalfa and pea, in seeds like cotton and Indian corn, in some fruits like bananas, in egg-yolk and many animal tissues. If twenty-five milligrams of wheat-germ oil be mixed daily with the food of a rat that is with young, the development of the young ones is very successful and normal birth results, but this will not be the case if the hypothetical substance is not present in the diet. Even five times as large a quantity of some other oil, such as peanut and flax-seed oil, with little vitamin E, will not compensate for the absence of the so-called vitamin of reproduction.

Puzzling Nutrition.—Could one not fatten stock on waste-paper? This question is suggested by Dr. L. R. Cleveland's success in rearing white ants or termites on a diet of pure cellulose. As a matter of fact they fed on Whatman filter-paper which had been extracted in hydrochloric and hydrofluoric acids and in ether.

More than ten thousand termites of two different species were used in the experiments, and they grew and multiplied for eighteen months without the slightest sign of malnutrition. Growth and multiplication occurred with the same rapidity as in the controls that received their normal diet of wood. Some of the colonies that were started with ten adults had after eighteen months more than two hundred half-grown individuals. The weight had increased forty times on a diet of filter-paper!

Many herbivores feed mainly on carbohydrates, such as sugar, but that is very different from a diet of pure cellulose. There are many extras in the herbivore's diet of grass or clover. Yet the herbivores do utilise much cellulose, and in doing so they seem to be indispensably helped by Bacteria and Infusorians in their food-canal. It is therefore interesting to notice that all the wood-eating Termites that have been examined contain an abundance of intestinal Infusorians (of remarkable beauty, like those of a horse's stomach), which have been proved to help in the utilisation of the dry-as-dust food. Similarly, in many wood-eating insects, like the larval death-watch or bookworm, there are partner yeast-plants which seem to have a fermentative action on the contents of the food-canal. Many cases are now known of this kind of vital partnership or symbiosis, but we should like to hear more about growing fat on filter-paper.

OTHER EVERYDAY FUNCTIONS

CIRCULATION OF THE BLOOD.—What should everyone understand in regard to the circulation of the blood? The use of the blood in an ordinary backboned animal is fivefold. (1) It distributes through the body the digested food by which the living tissues are kept in repair and by which the engines of the body, the muscles, are kept able to continue contracting. (2) It carries the oxygen quickly from the place of capture, say the lungs, to the place of combustion, say, the muscles; and it likewise carries the carbonic acid gas from the place of formation, say, the muscles, to the place of liberation, say, the lungs. (3) With the help of the lymph, which bathes the tissues very intimately, the blood collects the soluble nitrogenous waste, and takes it to the filters—notably the kidneys—by which it is excreted. This fine nitrogenous waste is partly due to the wear and tear of the living tissues and partly to the unused residue of digested nitrogenous food distributed by the blood. (4) From the ductless glands, or organs of internal secretion, such as the thyroid gland and the suprarenal bodies, the blood carries away certain potent chemical messengers or hormones which are distributed throughout the body, regulating

the various functions, and making the body more of a unity. (5) The blood has also a protective rôle, for among the white blood corpuscles there are some called "phagocytes" which are able to engulf and digest invading microbes. These phagocytes may leave the blood-vessels altogether and serve as a mobile bodyguard, and they also help in processes of wound-healing and the like. Moreover, some of the white blood corpuscles are able to form antibodies in the fluid or serum of the blood which counteract poisons. It is plain, then, that the blood is a very important fluid-medium, from which every part of the body takes and to which every part likewise gives. It is indispensable that it should be kept in circulation and that with rapidity.

What Harvey showed was that the blood moves quickly round in a circle, from the heart to various parts of the body and back again to the heart. But this needs further clearness.

There are two pumps side by side in the heart of any of the highest Vertebrates—the birds and the mammals. The right pump (or ventricle) drives impure blood to the lungs, whence there is a return of pure blood to the left receiving-chamber (or auricle) of the heart.

From the left auricle the purified blood, i.e. relatively rich in oxygen and with little carbon dioxide, passes into the left ventricle, which drives it to the body by the arteries. The arteries end in fine capillaries which penetrate everywhere, bringing the tissues what they need. From the arterial capillaries the blood passes into venous capillaries, as Malpighi first discerned, and thence into the veins, which bring it back to the right auricle of the heart.

The left pump of the heart drives pure blood (*a*) to the tissue of the heart itself, for the engine itself must be kept effective; (*b*) to the stomach and intestine; (*c*) to the kidneys; and (*d*) to the head, trunk, limbs, and body generally.

The impure blood from the head region is brought back to the right auricle of the heart by superior veins (superior venæ cavæ), and from the posterior body by a large vein (inferior vena cava). Into this posterior vein there also passes (1) by the renal vein, the blood which has been filtered in the kidney as regards its nitrogenous waste-matter, (2) by the hepatic vein the blood from the liver, which mediates between the general circulation and the portal system, bringing in the digested proteins and carbohydrates from the stomach and intestine, and (3) the blood from the tissue of the heart itself.

The vessels which bring back blood to the heart are the veins, and all of them carry venous or impure blood except the pulmonary veins from the lungs, which bring the oxygenated blood into the left auricle. The vessels which carry blood from the heart are the arteries, and all of them carry pure blood except the pulmonary

arteries, which bear the impure blood from the right ventricle to the lungs.

THE SPLEEN.—It is difficult to believe that Aristotle, surely one of the best brained of men, did not know what the brain is for. Yet he seems to have been so far from the error of a later disciple, who said that the brain secretes thought as the liver does bile, that he speaks of the brain secreting mucus! The fact is that Aristotle thought of what we call the functions of the brain as having their seat in the heart.

It is much easier to understand the long-continued obscurity in regard to the spleen, for its functions are intricate and elusive, not indicated like those of the brain by the associated nerves, or like those of the heart by the associated blood-vessels. It is only in recent years that it has become possible to speak with much definiteness regarding the rôle of the spleen, and even now the doctors differ. All are agreed, however, that their predecessors were wrong; and there is no doubt that we must entirely dismiss the libel that the spleen has to do with bad temper. We read in old books that the judge was suffering from a bad attack of the spleen, and consequently pronounced very severe sentences. Or, again, we read that the irascible master vented his spleen on his servants. No doubt a disturbance in any organ may be correlated with irritability of temper, but there is no particular warrant for blaming the spleen. Indeed, it is more innocent of offence than many another structure.

In most backboned organisms, from skate to man, the spleen is a deep red body situated to the left of the stomach. It is a somewhat spongy organ, for it is traversed by a network, partly muscular, in the meshes of which there is a pulp consisting of various kinds of cells. The muscular tissue is of the unstriped or slowly contracting type, and its ceaseless contractions and relaxations help to keep up an ebb and flow of blood in the spleen. Thus we might almost think of the spleen as a minor and accessory heart, all the more since it is a reservoir for red blood corpuscles. The rhythmical compressions and dilatations of the spleen, brought about by contractions and expansions of its muscular tissue, take place about once a minute, and are under the control of nerves from the spinal cord and from the sympathetic nervous system. But these big waves are made up of smaller waves, and these of smaller wavelets still, corresponding respectively to the breathing movements and the heart-beats. But the activity of a skate's spleen is apparently much less intense than that of a mammal.

An interesting feature is that while the arteries and veins of the body must be thought of as forming a closed system, the ends of the arteries being connected by capillaries to the beginnings of

the veins, this is not quite true of the spleen. For the splenic arteries end in an open brushwork of capillaries leading into spaces in the pulp, from which another set of open capillaries lead into the splenic veins. Thus it is possible for particles and corpuscles in the pulp to be swept away in the ceaseless ebb and flow. There is no doubt that this once-a-minute compression and dilatation of the spleen involves a considerable amount of internal work, and is of great importance in keeping up a continual passage of blood in and out of this hard-working organ.

In embryos and very young stages of backboned animals the spleen is one of the places where red blood corpuscles are made. But while this function usually persists throughout life in fishes and tailed amphibians, it seems normally to dwindle away in frogs, reptiles, birds, and mammals. In the last-mentioned the formative function may be in certain cases reawakened; but this never occurs in birds, though their blood is peculiarly rich in red blood corpuscles.

But the spleen is not only a cradle, it is a destructor. Many of the worn-out red blood corpuscles are disintegrated in the spleen of birds and mammals; while others seem to be so debilitated in passing through the splenic sponge that it is easy for the liver to give them a *coup de grâce* when they come to it in the course of their circulatory journey.

Another function which is usually ascribed to the spleen is the making of white blood corpuscles; but we infer from the recent very careful review by Skramlik that the evidence hardly justifies us in calling this rôle more than "very probable". Perhaps the white blood corpuscles are detained for a time in the prison of the spleen and are then liberated again in large numbers.

But this by no means exhausts the rôle of the spleen. For in most backboned animals, if not in man, the spleen has a share in changing the nitrogenous waste-products and the nitrogenous surplus products into substances like uric acid, which can be readily filtered out by the kidneys. Then again it seems that the spleen shares in the iron-cycle; that is to say, the iron which is set free in the disintegration of the hæmoglobin of the red blood corpuscles may be temporarily stored in the spleen and then given up again for re-utilisation.

Thus while it is true that removal of the spleen is not fatal, because of vicarious functioning on the part of the lymphatic glands, there is no doubt as to the importance and value of the organ, or as to the manifoldness of the rôle that it discharges. It is to be thought of as an active and sensitive organ, thrilling with rapid change to corporeal and external stimuli. Thus when a stickleback or an eel passes from fresh water to the sea, the weight of the spleen is reduced to about a half in twenty-four hours. There are interesting differences in the spleens of different animals which one

should be able to interpret. Thus the relative weight is less in marine fishes than in freshwater forms, and carnivorous mammals generally have a larger spleen than the vegetarians. But this must not be used as an argument either for or against humanitarian diet!

THE BIOLOGY OF EXCRETION.—A living creature is assuredly more than an engine, for it exhibits activities which cannot be adequately described in terms of mechanics and dynamics. Organism transcends mechanism. And this conclusion stands firmly on legs of its own, apart from the obvious fact that in higher animals there is a mind that counts for much, even in everyday affairs. None the less it is very useful to think of the living body as a number of interlinked engines that work into each other's hands, so to speak; for a living body is engine-like in being a material system adapted for the economical transformation of matter and energy. Let us pursue the analogy in regard to the waste-products that are formed by engine and by body alike.

A hard-worked engine soon accumulates some unused or unusable remains of the fuel, and these have to be reckoned with. But there is also a subtler kind of waste that is due to the wear and tear of the active parts. This is not so readily dealt with, and here the living body is far ahead of any engine in having remarkable powers of self-repair. In the living body there is often much quite unused fuel or food, and there are also the results of the chemical disruption of this fuel. Thus carbon dioxide is the familiar gaseous waste-product that results from the ceaseless combustion or oxidation of the nutritive carbon compounds. Everyone knows how it is got rid of on the internal surface of the lungs in higher animals, and in other ways in lower animals, for instance, by gills or by the skin.

But if we keep by itself the getting rid of the poisonous carbonic acid gas, and also the getting rid of undigested or undigestible food in the alimentary canal, we may narrow our inquiry to the nitrogenous waste-products which have to be filtered out of the animal, or otherwise summarily dealt with, if life is to continue smoothly. The nitrogenous waste is partly due to the wear and tear of the protein framework of the cells, and might be compared to the minute particles of steel found in the lubricating oil of the engine. But it is also, and in great part, due to a surplus of unused, though digested, nitrogenous food which has passed into the blood. This part of the nitrogenous waste might be compared to the products formed in an oil-engine when the combustion is not thorough enough, or when the proportions of the factors in the combustion are not well adjusted. To the filtering out of the nitrogenous waste-products of twofold origin, physiologists usually restrict the term excretion.

To understand this even a little, it is necessary to proceed patiently and to state a few chemical facts. The proteins of our food, such as the casein of cheese, the gluten of wheat, the vitellin of yolk of egg, are nitrogenous carbon compounds, and they are digested in the food-canal into the simpler amino-acids, which are absorbed into the blood. In part these go to repair the wear and tear or to furnish material for growth; but they are also in great part broken down into ammonia, which is apt to be poisonous, and some derivative of a fatty acid. The latter is burnt up to supply bodily energy; the former is converted into urea, and this is in great measure the work of the hard-worked liver. What the liver prepares for excretion, such as urea in mammals, is filtered out by the kidneys. The preliminary process of splitting off the ammonia and forming a fatty acid is called de-amination. The second step is the liver's conversion of ammonia into urea. The third step is the actual elimination effected by the kidneys.

It is of theoretical interest to distinguish the endogenous chemical routine by which proteins, changed into amino-acids, are used to furnish material for growth and for repair, from the exogenous metabolism by which amino-acids are de-aminated to supply energy by the burning up of the resulting fatty acid. Along both lines the same final result may be reached, namely urea. But it is practically important, for health reasons, to realise that the nitrogenous waste-products that are filtered out may be the ashes of the living fire, or may be the direct and indirect results of the wear and tear of tissues. It may seem absurd to talk of a fluid as "ashes", but the various states of matter readily pass into one another, and everyone who has kept birds knows that the nitrogenous waste-products from the kidneys are semi-solid. They form most of the guano of the crowded bird islands of Peru, for the undigested residue from the food-canal is much less important.

Two points stand out prominently, one practical and the other theoretical. The practical point is the danger of giving liver and kidneys too much profitless work to do by taking in far more nitrogenous food than is needed by the requirements of the body either for repair or for energy. The theoretical point is that while urea is the commonest nitrogenous waste-product in mammals, amphibians, and fishes, and uric acid is characteristic of birds and reptiles, there are other kinds of ashes, such as salts of ammonia, in some backboneless animals. It is a question of high biological interest whether skeleton-making in animals like sea-urchins and molluscs, and pigment-making in others like butterflies, may not express profitably regularised ways of dealing with the ashes of life's fire.

So far, a mere outline of the animal's method of dealing with nitrogenous waste-products—a problem that has been much

illumined by the investigations of Prof. Cathcart of Glasgow. But let us now turn to plants. Have they any ashes from their hidden fires, and if so, do they get rid of them? The old view that plants, being half asleep, do not form nitrogenous waste-products like urea is contradicted by more careful biochemistry, for urea itself has been demonstrated in some plants, and likewise the frequent occurrence of allied substances like asparagin, glutamin, and allantoin. Of great interest also is the discovery of a urea-fermenting ferment (urease) in many higher plants, as well as in many bacteria. Living involves the breaking down of proteins, and this involves the formation of ammonia. But ammonia, above a narrow limit of quantity, is a cell-poison, so in the higher animals it is changed into the relatively harmless urea or uric acid, while in some lower animals it is neutralised in other ways. What happens in ordinary plants is profoundly interesting and very different. For many, if not most animals, it is profitable to get rid of the nitrogenous waste-products (urea, etc.) as soon as possible; for fresh nitrogen supplies are readily available in the food. But it is far otherwise with ordinary green plants that have to find their nitrogenous food sparsely in the form of nitrates (like saltpetre) and so forth in the soil. That leguminous plants with their symbions are able to tap the nitrogen supply in the atmosphere is no more to the point at present than are other exceptional cases like insectivorous plants and those that feed on decaying organic matter. An ordinary animal is apt to suffer from nitrogen-excess, and man most of all; but an ordinary plant is apt to suffer from nitrogen-deficiency. This brings us to recognise the excellence of the plant's chemical régime, for substances like asparagin and glutamin, which are widely distributed, seem to be combinations which take the poisonous edge off the waste ammonia. In many a member of the fungoid class the same rôle is discharged by urea itself. Thus plants and animals meet in the mushroom!

But there is another adaptation besides drawing the ammonia's teeth, for, as Kiesel and others have shown, the ammonia, rendered harmless by combination, can be remobilised when nitrogenous material is required by the plant in the building up of fresh protein substances. This is the significance of ferments like urease and asparaginase within the plant, that they re-liberate the ammonia when it is needed. Thus the plant is more economical than the animal, since it can use its waste-products as a reserve. It is plain that this locking up of the ammonia, and its liberation again, must involve a very strict regulation of the doors, but regulation is the inmost secret of life.

Finally, see how the plant cell's substantial cellulose wall (and so the tree's wood) is really an excretion of incompletely oxidised material, done with so far as the protoplasmic metabolism is con-

cerned: necessary though it be for the cell's protection, the plant's coherence, water-passage, etc. So when we burn our wood, we warmly realise how much fuller is our animal oxidation, how great the gain to our animal energies and activities accordingly.

REGULATIVE SYSTEM

INTEGRATION.—Sponges are animals which often show detailed complexity, e.g. in their water-canal system, their component cells, and their loose spicules or coherent skeleton; but they have a minimum of *integration*. That is to say, the body is but slightly unified; a large piece can be cut off without making any appreciable difference; and it may be noted that sponges have no specialised nerve-cells at all. Around the larger exhalant openings or oscula there are in some cases unstriped muscle-cells which contract when touched, and might therefore be called neuro-muscular—receptors and effectors in one, but there are no nerve-cells—a fatal defect, prohibiting integration. In an animal at a much higher level, the Portuguese Man-of-War (Physalia), a colony of transformed medusoid individuals, sometimes of at least five different kinds, there is unified movement; the various "swimming-bells" work in harmony, being regulated by a network of nerve-cells extending through the colony. Yet there is no central nervous system, and many members of the colony can be cut away without any appreciable damage to the life of the whole. In the great majority of animals, however, from earthworm to elephant, from bee to bird, we have to do not only with differentiation or division of labour in various degrees, but with an increasingly unified control or regulation of the life of the body which is called integration. When we say that one animal is "higher" than another, we mean that it is more differentiated and also more integrated.

Some measure of integration is implied in the physical binding together of the body, for instance, by the possession of a dorsal axis or backbone to which the limbs are usually attached; or by the grouping of the muscles, which often work together in contrasted harmony like the biceps and the triceps of the forearm, the one relaxing as the other contracts. The same result may be reached by the possession of a coherent carapace or shell, as in crab or snail, to which some of the muscles of the animal are intimately attached. In various ways, then, there is brought about a measure of physical integration.

Much more important, however, is the integrative influence of the nervous system, of which we have already spoken. This is increasingly integrative (*a*) in proportion as the nerve-fibres reach to every part of the body, even the most outlying, and (*b*) in pro-

portion as the nerve-cells become centralised in structures like the brain and the spinal cord. The life of a higher animal depends on the timing and tuning, even up to orchestration, of countless reflexes. Nervous stimuli from the outer world or the organs of the body affect the cells of the centres, and evoke efferent impulses which effectively control muscles and glands and other parts.

With this nervous integration in the big-brained animals must be associated, though the relation remains a riddle, a mental or psychical integration; for it is difficult, some would say impossible, to doubt that a dog, for instance, may be actuated by a perceived purpose, and there is nothing that integrates life more powerfully. The physiologist, like the physician, has often to take account of the *esprit de corps* in a quite literal sense.

But another important kind of integration is effected by the blood, the common medium (along with the lymph) from which all the cells of the body take, and to which they all give. As we have already seen, the blood is a food-distributor, a gas-carrier, and a waste-collector; it is also a bearer of the migrant amœboid cells called phagocytes, which play an important part in the internal defences of the body, as is also true of many of the cells lining the vast interior area of the capillaries. Moreover, the blood is able to manufacture counteractives or anti-bodies, which act as antagonists to poisons, though we have as yet no clear knowledge of how they effect this. Thus the blood has a manifold regulative influence.

It may be useful to think for a moment of the familiar reaction of sweating, which is an automatic way of preventing the temperature of a mammal's body from rising too high in very warm weather or in the course of very hard work. The sweat-glands in the skin are stimulated to increased activity; they pour out more water, the evaporation of which serves to lower the temperature. The stimuli come to the sweat-glands by nerves which may accompany the peripheral blood-vessels or may be independent of them; and these nerves come from special centres in the spinal cord and in the medulla oblongata. But how do these nerve-cells become alive to the fact that sweating is called for? The answer illustrates what we mean by the integrative action of the blood. The blood that has become overheated flows through the central nervous system and excites the specialised nerve-cells of the regulative ("thermotaxis") centre; and thence nervous impulses pass to the cells of the sweat-glands, arousing their greater activity. This is not, indeed, the whole story, for the blood which we have simply called "overheated" may differ from the normal in containing more than the usual quantity of carbonic acid; and it does differ from the normal in its content of hydrogen-ions. But the general fact of importance here is simply the effectiveness of the integrative action of the blood.

A notable extension of this general idea of the blood as a corre-

lating medium has resulted from the investigations of the last thirty years on the secretions of the ductless glands; and to the re-consideration of these we must now pass.

INTERNAL SECRETIONS.—Claude Bernard seems to have been the first physiologist to realise with clearness the importance of the "ductless glands" or glands of internal secretion. He refers to the secretion produced by such organs as the thyroid body, the suprarenal capsules, and the spleen; but it should be noted, perhaps, that he applied the term "internal secretion" to grape-sugar, which passes, as he showed, from the liver-cells into the blood. This use of the term would not be accepted to-day, for it is now restricted to chemical agents that have a specific effect on certain tissues or processes; it does not include general nutritive material, or the mere waste-products, or the products of glands with ducts.

But Claude Bernard's suggestion did not attract much attention, and more stimulating to research was Brown-Sequard's demonstration of the tonic effects of testicular extract—a scientific vindication of ancient medical prescriptions, such as the use of the stag's testes as an aphrodisiac. But Brown-Sequard was led by his experiments with testicular extract to a theory almost too generalised to mean much; he maintained that *all* tissues contribute to the blood something or other that is specific and important. This was too general a return to the old idea of a *consensus partium*, a functional correlation of the body effected by diffused "humours"; but even in this vague notion there was sound sense.

Some interesting historical notes are given by Dr. Swale Vincent in his scholarly treatise, *Internal Secretion and the Ductless Glands* (3rd ed., London, 1924). Thus as far back as 1775 Théophile de Borden spoke of each organ as the source of a "humeur particulière", which exerts an influence on the body generally; in 1801 Legallois discussed the relation between the different secretions (from *all* glands, however) and the varying composition of the venous blood; in 1852 W. B. Carpenter spoke definitely of the contributions made to the blood by the "vascular glands" (e.g. thyroid and suprarenal), along with which he included fatty tissue and the spleen. Very important, though forgotten till unearthed by Biedl, was an experiment made in 1849 by Berthold of Göttingen. He excised testes from young cockerels and grafted them on the wall of the intestine, with the result that the cockerels did not develop, as castrated males usually do, into capons, but grew into normal cocks.

The student will observe the increase of definiteness and precision that so often marks the emergence of a speculative idea into a substantial discovery. The general idea of correlation of the body is very old—familiar, for instance, to St. Paul, who speaks of the

various members having "a common concern for one another". The *consensus partium* that the old physiologists and physicians speak of, was attributed in the eighteenth century to pervading "humours" made by various organs, and not always distinguished from the blood itself. While the anatomists began to shift emphasis from the blood to the nervous system as the agency in correlation, increasingly giving the latter the credit, the doctrine of diffusing substances still kept its footing in the more physiological minds. Thus Treviranus, writing about 1801, declares that "each single part of the body, in respect of its nutrition, stands to the whole body in the relation of an excreting *substance*". Gradually the "humours" were replaced by "internal secretions"; gradually the list of these was criticised and sifted; gradually the different secretions—the hormones—have been separated, and their specific effects tested. Even in Invertebrates the discovery of hormones has begun, notably in the pigmented packing-tissue of the leech. Even in plants we begin to hear of them, notably in the ultra-sensitive Mimosa.

NATURE OF HORMONES.—The word "hormone" (*hormao*, to stir up), which means excitant, was suggested by Hardy, and accepted by Starling in 1902, as a name for the characteristic product or "chemical messenger" of a ductless gland. "By the term 'hormone'", Starling said, "I understand any substance normally produced in the cells of some part of the body and carried by the blood system to distant parts, which it affects for the good of the organism as a whole." But as the word hormone was, to begin with, used somewhat widely for any excitant substance in the blood (including carbonic acid!), Sir Edward Schäfer proposed the term "autacoid" (which means self-remedy) for the specific products of ductless or endocrine glands. An autacoid is defined as "a specific organic substance formed by the cells of one organ and passed by them into the circulating fluid to produce effects upon other organs similar to those produced by drugs". Since the effects may be in the direction of excitation or in the direction of restraint or inhibition, Schäfer proposed to call the excitatory autacoids hormones in the stricter sense, and the restraining or inhibiting autacoids chalones (which means slackening). Biedl has made the interesting suggestion that the former—"erregende Hormonen"—induce katabolic changes, while the latter—"hemmende Hormonen"—induce anabolic changes; but this has not been substantiated.

At this point it is historically appropriate, as well as useful for clearness, to refer to the hormone "secretine", which Bayliss and Starling discovered in 1902, and to which they originally applied the term "chemical messenger". Secretine is produced in the presence

of acid by the cells lining the duodenum, that is to say, the beginning of the small intestine. It is carried away by the blood-stream and passes in due course round the body. But it seems to have no effect anywhere except in the pancreas, and, to a slight extent, in the liver. It increases the secretion of pancreatic juice, the most potent of digestive juices, and this passes by the pancreatic duct into the duodenum, there promoting digestion. There is also to a less degree a stimulus to the secretion of bile. When a meal is in process, or it may be in prospect, there is by means of the hormone secretine a preparation for its digestion. This illustrates physiological correlation; the mucous membrane of the food-canal and the pancreas work together in vital partnership for the digestive good.

How is a conclusion of this kind established, seeing that secretine is an invisible substance that leaves no track? The hormone was obtained by boiling the mucous membrane with dilute hydrochloric acid and afterwards neutralising and filtering. The hormone obtained in the filtrate was then injected into the blood, and this was followed by increased production of pancreatic juice. It was also known that washing the duodenum with dilute mineral acid would provoke increased secretion of pancreatic juice—doubtless through the increased production of secretine. It may be mentioned that another hormone analogous to secretine, but acting on the gastric glands of the stomach, has been extracted (Edkins, 1906) from the stomach lining towards the pyloric end.

But the hormones that have been most studied are those of the thyroid gland, the suprarenal capsule, the pituitary body, and the reproductive organs. Before we consider these and others separately can we form any clearer picture of hormones in general?

(1) In most of the glands that get rid of what they produce by a duct, or on a free surface, the secretions are of the nature of ferments or enzymes. They are probably of a protein nature and they are easily destroyed by hot water. But hormones or "internal secretions" of ductless glands, whatever they may be, are not enzymes; and for the most part they are not destroyed even by boiling. They resemble enzymes in being able to act in minimal quantities; but they differ from enzymes and resemble vegetable drugs (e.g. alkaloids) in the rapidity with which they exert their influence.

(2) Hormones are dialysable, and some of them have been isolated in crystalline form. Adrenalin, which is produced by characteristic cell-groups in the centre of the suprarenal capsules, has been artificially synthesised; and so has thyroxin, the iodine-containing hormone of the thyroid gland. Since hormones pass readily through the walls of the blood-vessels they must have a low molecular weight. Although it contains iodine, thyroxin (like adrenalin) is related to tyrosin (see *Chemistry of the Cell*). It is probable, how-

ever, that the various hormones differ widely from one another in chemical composition.

(3) A negative character which they all exhibit is that they do not evoke the formation of anti-bodies or counteractives in the blood. That would indeed be a contradiction in terms!

(4) Hormones are mainly known by the consequences that follow their artificial introduction into the body, either by the injection of extracts or, in some cases, by their introduction along with the food. Another method of discriminating the function of a hormone is to observe the changes that follow the removal or degeneration of the ductless gland that produces the substance in question. Both methods require careful handling, for they involve serious disturbance of physiological balance. Even if an injection of pituitary body always produces a particular effect on the body, it does not necessarily follow that this indicates the normal use of the pituitary hormone in the everyday normal life of the organism.

The problem is also complicated by the facts that one and the same endocrinal organ may produce more than one hormone, and that one and the same hormone may produce several effects. Some hormones seem to produce opposite results in different parts of the body. Thus, as Schäfer points out, adrenalin causes contraction of the smooth muscle-cells of the blood-vessels, but inhibition in those of the intestinal wall. "The possibility of the same autacoid substance acting under some circumstances as a hormone or excitant, and under other circumstances as a chalone or depressant, must be borne in mind. This, indeed, serves to illustrate the drug-like nature of these principles, for such inversion under different circumstances is known to occur with some alkaloids." From what we have said the student will infer that it is necessary to be very careful in making general statements in regard to hormones.

THE THYROID GLAND.—This ancient structure, found throughout Vertebrates, is represented in man and mammals by a small reddish paired body lying beside the larynx. It has a very rich vascular supply. In birds it is situated in front of the heart, close to the origin of the carotid arteries. In lizards it is usually a paired body half-way up the windpipe; in Bony Fishes or Teleosts it is paired and situated near the first gill-arch; in the skate it is unpaired and situated immediately behind the lower jaw. In short, it occupies diverse positions in the region of the neck in different types of Vertebrates.

Its development is very interesting, for it always arises as a mid-ventral pouch from the wall of the pharynx. This outgrowth becomes constricted off from its origin, though the stalk connecting it with the pharynx or the posterior floor of the mouth may persist for a considerable time. It usually becomes a paired body; it becomes

complicated by forming little buds or vesicles; it ceases to be connected with anything but blood-vessels; it becomes a very typical endocrinal or ductless gland.

The key to the evolution of the thyroid is found in the lamprey, for in its larval form (the Ammocœte or "niner") the thyroid is a mid-ventral gutter-like fold of glandular and flagellate cells which remains open to the pharynx. This is undoubtedly homologous with the ventral pharyngeal fold, called the endostyle, which persists throughout life in Amphioxus (lancelet) and Tunicates (sea-squirts). Some zoologists, indeed, would trace it farther back still to the ventral portion of the pharynx in the half-chordate, half-wormlike pioneer types known as Enteropneusta, of which Balanoglossus is a common example in many seas.

As the larval lamprey continues its slow development, the communication between the thyroid diverticulum and the pharynx is gradually reduced, till eventually a narrow slit becomes a pore, and even this disappears when the "niner" metamorphoses into a lamprey. The organ divides up into numerous closed vesicles, and it is a suggestive fact that these, like the vesicles of other thyroids, continue making a mucous colloid material like that employed in entangling food-particles in lancelets and Tunicates. The function persists though the material produced can no longer be exuded.

This interesting chapter in evolution, first outlined by W. Müller in 1871, discloses a good instance of change of function. What was originally a glandular organ connected with the food-canal has become from fishes onwards a ductless gland, and that hormone-producing.

Closely associated with the thyroid in man are four minute "parathyroids", little studied except in mammals. They develop as outgrowths from the third and fourth gill-clefts on each side, that is, from the clefts that give rise to another difficult organ —the thymus. The parathyroids are also endocrinal, and the hormones they produce are different from those of the thyroid proper, but their still obscure function will be considered later.

When the thyroid degenerates in a young animal or is removed, the result is arrest of growth, especially of the skeleton; also an arrest of development in the cells of the cerebral cortex, a flabbiness in the muscular system, a slowing of the development of the reproductive organs, and various other symptoms which are summed up in the word *cretinism*. In the case of children there is an arrest of bodily and mental development; the child remains infantile, even if it ceases to be in years a child. These abnormal conditions may be alleviated, indeed in many cases cured, by adding to the diet preparations of sheep's thyroid, or some form of thyroid extract, or artificially synthesised thyroxin.

A disease of adults due to thyroid deficiency or degeneration is known as myxœdema. It is marked by thickening and coarsening of the skin, loss of hair, in many cases subcutaneous fattening, reduced metabolism, low temperature, diminished sexual activity, dullness of sense and mind. As with cretinism, restoration to health may be secured by adding thyroid gland or its extracts to the diet, but intermission of the treatment may be followed by a return of the symptoms.

In the huge enlargement of the thyroid gland, which is called goitre, there is often, though by no means always, an abundance of secretion, as might be expected from a big gland. But as the symptoms are in the majority of cases like those associated with thyroid deficiency, the probability is that the specific hormone is absent or scanty.

An exaggeration of the specific thyroid secretion (hyper-thyroidism) is associated with exophthalmic goitre, so called from the protrusion of the eyeballs. It is marked by increased metabolism (especially nitrogenous), irregular pulse, throbbing, excitability, restlessness. The disease occurs most frequently in females. A consideration of diseased conditions associated with exaggerated or deficient thyroid activity throws light on the normal function of the gland; and it has this wider biological interest, that sundry peculiarities of animals, such as the coarseness of the elephant's hide, the whale's blubber, the relative hairlessness of the rhinoceros, the prominent eyeballs of the mouse, besides more general features like dwarfness and nervousness, may very possibly be associated with variations in their thyroids. In other words, it is worth considering the possibility of the variation and racial normalising of hypo- and hyper-thyroidism in various types of animals. The general theory of somatic variations being due to changes in endocrinal secretion is considered under Evolution.

The specific autacoid of the thyroid has been isolated, crystallised, and analysed by Kendall (1919), who calls it thyroxin. It is an iodine-bearing derivative of a protein (tyrosin), and its chemical structure is expressed in its chemical name tetraiodo-hydroxyphenoxy-phenyl-amino-propionic acid! There may well be room for variability in such a complex body as this.

The everyday use of this thyroid hormone is probably to increase the excitability of nerve-cells; but it appears to exert a regulating influence on many parts and processes. The autacoid of the parathyroid is believed by some to be chalonic, putting a check on nervous activity, indirectly by controlling the amount of calcium in the fluids of the body. Thus some regard thyroxin as a general catalyst which increases the rate of the fundamental metabolic processes. Similarly, some would say that the parathyroids, so intimately mingled with the thyroid, are not strictly endocrinal,

but have as their chief function that of neutralising the poisonous substance guanidine, which is formed from the creatine of muscle.

THE SUPRARENAL OR ADRENAL CAPSULES.—These are present in most Vertebrate animals, and occur in man as two cocked-hat-shaped bodies, one on the upper border of each kidney. They have a remarkable structure and a remarkable development. In mammals they show two very distinct parts, a central *medulla* and a peripheral, often yellowish, *cortex*, differing in minute structure. The medullary substance arises in development from the sympathetic nerve ganglia; while the cortical substance arises between the two kidneys from a number of thickenings of the epithelium that lines the body-cavity. Thus the suprarenal or adrenal apparatus in higher Vertebrates is an intimate union of a mesodermic and an ectodermic primordium.

In birds and reptiles the suprarenals are elongated and situated near the reproductive organs; in Amphibians they lie as a yellowish streak along the ventral surface of the kidney. But it is their condition in Elasmobranch fishes that is most illuminating, for there the two parts are separate from one another. In sharks and skates the cortical substance is represented by yellow *interrenals* and the medullary substance by independent *chromaffine* organs. A remarkable feature is that when the two fuse in Amphibians the chromaffine component encloses the other—just the opposite of the final state of affairs in mammals! There also the chromaffine tissue is outside the cortical tissue to begin with.

A pathological condition of the suprarenal apparatus in man is associated with Addison's disease, marked by a bronzing of the skin; the removal of the organs from a mammal is always fatal, but it is the mysterious cortex which is essential for life. The specific hormone is adrenin or adrenalin, and it is produced by the medulla only, and it may be noted that it is also produced by isolated patches of chromaffine tissue that sometimes occur on the peritoneum or along with the sympathetic ganglia. The everyday physiological importance of adrenalin is to keep up the tone of the muscles, including those of the blood-vessels, and it does this through the endings of the sympathetic nerves. The amount that passes into the blood-stream is affected by the splanchnic nerves, and these again are excited by emotions such as rage and fear. In the case of the angry man, the emotion excites the splanchnic nerves, which stimulate the outflow of adrenalin. When the hormone passes into the blood, it improves the vigour of the heart and the tone of the muscles; it increases the amount of sugar in the blood, and increases metabolism; in short, it prepares the body for a fight. It also appears to increase the coagulability of the blood, which will be of advantage if there is a wound.

In the familiar case of the cat molested by the dog, the increased flow of adrenalin has among its numerous effects the erection of the hairs on the skin, through the contraction of the minute erector muscles at their base.

Adrenalin is chemically related to tyrosin, a common amino-acid. It has been prepared synthetically. Its use in stopping nose-bleeding and the like is due to its constricting action, through the sympathetic nerve endings, on the small blood-vessels. Its potency is so great that one part in a million will work.

The use of the cortical substance of the suprarenal bodies is not yet clear, but it appears to be essential to life. It contains in droplet-form large quantities of fatty and lipoid material (cholesterol and phosphatides), and many physiologists believe that it has to do with the metabolism of these substances, which occur abundantly in the gonads and in the central nervous system. There seems to be a close correlation between the cortical substance and the reproductive organs, but there is no convincing evidence of the presence of a specific hormone.

THE PITUITARY BODY.—One of the most remarkable organs in our intricate equipment is the pituitary body—far older than hair, far older than fingers. It develops from an upgrowth from the mouth (the oral part of the hypophysis) which meets and unites with a diverticulum growing downwards from the floor of the second region of the brain behind the cerebral hemispheres. It is ensconced in the sella turcica of the basisphenoid, a little saddle-shaped depression in one of the bones in the base of the skull. Although it is a small organ, it has a complex structure, and consists in mammals of four distinct parts which differ in microscopic details. In man it is about the size of a small kidney bean.

In the older books on anatomy and physiology the pituitary body is disposed of in a few lines; and the remark is sometimes made that its function is quite unknown; for the idea of the ancients that it secreted the nasal mucus or pituita is of course quite erroneous. But all this neglect is a thing of the past, as may be indicated by Mr. G. R. de Beer's book of over a hundred pages devoted wholly to the *structure* and *development* of the pituitary body throughout the Vertebrate series. A similar book might be written on the functions of the pituitary body, which are not one but many. The recent concentration of attention on the little organ in question is due to the fact that its secretions or hormones are essential in regulating or harmonising the vital functions of the body. A removal of the pituitary body from an animal means cessation of growth and of sexual activity, and leads to various disorders of metabolism.

The remarkable development of the pituitary body demands further description. On the one hand there is a downgrowth from

the floor of the 'tween-brain—that small but important second region of the brain, from which grow out the eyes and the pineal body. But in the second place there is in development an earlier hint of the pituitary body, namely, a pre-oral ingrowth of the outer layer or ectoderm of the embryo. This ingrowth is solid in lampreys, Bony Fishes, and amphibians; it is hollow in gristly fishes, and in reptiles, birds, and mammals. It may arise within the depression that forms the front of the mouth, but it has no real connection with either mouth or nose. There are strong reasons for regarding this ingrowth—the hypophysis, as it is technically called—as represented by a ciliated pre-oral pit in the lancelet or Amphioxus. If so, it is clearly one of the most ancient structures in our body.

Whatever be its historical origin there is no doubt as to the individual development of this part of the pituitary body; it is an insinking of the superficial embryonic layer or ectoderm. Two things happen. First, it comes into connection with the little downgrowth (the "infundibulum") from the 'tween-brain; and second, there is an acquisition of the endocrine mode of internal secretion. The result is an intricate organ, partly nervous, partly glandular, partly vascular—the pituitary body. In his monograph (*The Anatomy, Histology, and Development of the Pituitary Body*, Oliver & Boyd, 1926), Mr. de Beer gives an eloquent genealogical tree showing the evolution of the organ through the Vertebrate series. It is hardly a story that he who runs can read; but it rewards one to spend some time in its scrutiny, for it shows very vividly how a couple of small growths, neither very promising to start with, unite to form an organ that evolves into one of the main regulators of our life.

Experiments have confirmed a conclusion reached from the study of disease, that the anterior part of the pituitary body, which is of oral origin, produces a hormone which controls growth—of bones in particular. Inadequacy in the supply of secretion leads to abnormal dwarfs; exaggeration in the supply leads to abnormal giants. This nanism and gigantism must be distinguished from the occurrence of healthy, well-proportioned, intelligent dwarfs and giants, who probably arise as germinal mutations, quite unconnected, it may be, with anything wrong with the pituitary body. In any case the pituitary body normally regulates the growth of the young organism; and there may be some fact behind the story that a candidate for a cadetship, whose only defect was being an inch below the standard of height, took a six weeks' course of pituitary extract and succeeded in adding the required fraction of cubit to his stature. *Ben trovato,* at any rate. It has been suggested that some of the extinct giant reptiles suffered from pituitary exaggeration; and that the elephant tribe have owed much to this too. Hormones of the anterior lobe also stimulate the ovary

to activity, hastening the development of the follicles and evoking a flood of the ovarian hormones.

The posterior lobe of the pituitary body is of cerebral origin, and although its minute structure is like degenerate nervous tissue there is a production of several hormones of great physiological potency. One of these causes the capillaries to contract and the blood-pressure to rise, and is thus naturally associated with increased renal activity. But the intricacy of these inter-relations is suggested by the fact that there seems to be an associated pituitary substance that *lowers* blood-pressure. It may be, however, that this substance is not peculiar to the pituitary body, but is common to many organs. Yet another complication is indicated by the fact that injury to the posterior lobe acts on the kidney and leads to diabetes insipidus, which can be relieved by pituitary injection. Another pituitary hormone has a general effect in exciting smooth or plain muscle to contraction, and is so potent that a solution of one part in a hundred thousand millions will work! Remarkable also is the influence that changes in pituitary secretion exert on the contraction and expansion of the dark pigment-cells (melanophores) in the frog's skin.

The active substances produced by the pituitary body have not yet been isolated, and there is no hint that they are represented outside the sub-kingdom of Backboned Animals. It may be noted that Prof. Herring of St. Andrews showed long ago that material from the anterior part of the pituitary body may pass into the cavity of the 'tween-brain, and thus into the cerebro-spinal fluid. At the same time, apart from the regulation of bone-growth, and perhaps the maintenance of capillary tone, it is difficult to say what everyday value should be put to the credit of the powerful secretions made by the pituitary body. For such influences as those mentioned on kidney activity and milk yield are demonstrated in experimental conditions, and we cannot at present say that pituitary secretion is concerned with kidneys, mammary glands, blood-pressure, and the like in ordinary normal life. It is therefore very satisfactory to find Hogben's and Winton's brilliant demonstration that pituitary secretion is the main factor in co-ordinating the everyday pigmentary responses that frogs and other Amphibians make to the changing conditions of their environment. Others have shared with these investigators in proving that the regulation of the normal colour-response in these animals is mainly due to fluctuating pituitary secretion. The mistake must not be made of arguing from the frog's colour-change to that of other animals, such as fishes (see section on Coloration).

CORPUS LUTEUM.—The egg-cells or ova of mammals appear within nests of cells in the ovary, called Graafian follicles, dis-

covered by Graaf in the seventeenth century and mistaken for the ova themselves. Each follicle is a nest with a cavity, and the egg-cell lies in the middle of a disc of cells at one side. The cavity contains a fluid, the follicular fluid, an exudate from the surrounding cells. It may be noted that the egg-cells of mammals (except the egg-laying duckmole and spiny ant-eater) are very small, much smaller than frog's eggs, which are about a tenth of an inch in diameter. The ova of the whale are no larger than "fern's seed"; those of a rabbit have a diameter of about $\frac{1}{250}$ inch.

When a follicle which protrudes on the surface of the ovary is ripe, it bursts, and the liberated ovum is caught by the apposed mouth of the oviduct, where fertilisation may take place. The fertilised ovum, beginning to develop, passes down into the uterus, where it is implanted and proceeds to give rise to an embryo.

But the burst follicle has a remarkable history. The follicle cells begin to grow and develop in an extraordinary way, forming large glandular cells of a yellow or reddish brick colour—the luteal cells. As the result a large vitally active body is formed—the corpus luteum, which protrudes on the surface of the ovary. There is strong reason to believe that this body liberates into the blood certain hormones which have a powerful influence on various parts of the mother's body.

There seems to be a tendency to overload the corpus luteum with functions in the way of preparing the mother-organism for pregnancy; and there is an obvious difficulty in the fact that some of the preparatory changes begin before active corpora lutea are present. Hence the importance of recent work by Allen and Doisy (1923), which goes to show that the *follicle cells* have a share in the preparation. During the growth of the Graafian follicle the follicle cells appear to secrete a hormone, which passes into the follicular fluid and thence into the blood. Experiments show that this follicular hormone (included in the fluid) can evoke some of the changes which were formerly put to the credit of the corpus luteum.

Some years ago Dr. Voronoff was impressed by the flabbiness, inferior intelligence, early senility, and relatively short life of Egyptian eunuchs, and attributed these features to the absence of the normal testicular hormones. Similarly he was impressed by the tendency to early decrepitude and the like in castrated mammals. So just as thyroid deficiency in man is counteracted by treatment with preparations made from the thyroid glands of mammals (or nowadays from synthetised thyroxin), Voronoff suggested that the experiment should be made of grafting reproductive glands into the ageing organism. The transference of a reproductive organ from one individual to another of the same species is no novelty; thus it was successfully effected twenty-five

years ago by Dr. F. H. A. Marshall, Reader in Agricultural Physiology at Cambridge, and it has been repeatedly successful since. But Voronoff was able to effect the transference of chimpanzee or of baboon testes into man, and apparently with very good results —as regards memory as well as muscles, as regards will-power as well as blood-pressure.

But most of Voronoff's successes (we know too little of the failures) have been between animals of the same species. Thus a decrepit ram, grafted at twelve years, renewed its youth in three months and was vigorous till it was twenty. Dr. Marshall vouches for the reinvigoration of an enfeebled Algerian bull, which was in good fettle four years after the graft. In the case of immature male sheep, whose reproductive hormones have not begun to tell, Voronoff claims that a testicular graft hastens growth and increases general vigour, affecting, for instance, the quality and length of the wool. But there are many possible snags in these investigations, and while the Austrian experimenter's work is of great interest, there is need for scientific caution. Let us hasten slowly.

ILLUSTRATIONS OF PLANT PHYSIOLOGY

In uniting Plants and Animals under the common title *Organisata* (1735), Linnæus was far ahead of his time, for it was not till about a century later that the fundamental unity of plant and animal life was generally recognised. That recognition was won by Claude Bernard's famous book, *Phénomènes de la Vie communs aux Animaux et aux Végétaux* (1879). The differences between plants and animals are great; but the resemblances are greater.

In our sketch of *animal* physiology we began with contractility and irritability—the power of movement and the power of feeling—and then proceeded to show how these "master-activities", as Sir Michael Foster called them, are kept agoing by the ancillary or sustentative functions of nutrition, respiration, excretion, and so forth. But while plants have their interesting movements and reactions to stimulus, their main activity is *growth*. The matter and energy of their income is mainly expended in adding to their size, which is in many cases slow of reaching a limit. Even when an individual plant remains small, there may be a lavish expenditure in discontinuous growth, which spells asexual multiplication. Though no doubt extreme, the Big Trees or Sequoias of California are but characteristic, with an enormous intake of matter and energy, sometimes prolonged well over three thousand years; and this is mainly expended in the attainment of a huge body which has to be lifted and held against gravity and wind, even to a height of 300 feet in the air. Whereas animals change most of the chemical

energy of their food into the kinetic energy of movement, usually locomotor, the essential feature of plant-life is the utilisation of food for increase in size and numbers. No doubt plants have their varied outgo of matter and energy, as in the transpiration of water-vapour, and in the transport from roots, through stem, to leaves; and the loss of parts—such as foliage, flowers, and fruits; yet the characteristic plant expenditure is in *growth.*

NUTRITION.—The popular notion of plant nutrition seems to this day too much inherited from that of Aristotle, with his unfortunate comparison of the plant to an animal burrowing for its food in the ground, and so with its foliage merely like hair or plumage! In later times, even with clearer perception of the main task of the roots, as for provision of water, the long persisting error became questioned and at length put to an experimental test, crucial and classic. Van Helmont took a small willow twig and planted it in a large pot of dry earth carefully weighed, kept it supplied with rain-water, and watched its growth year by year, until it was a little tree. Carefully removing this, he found its weight many times increased, yet the soil had only lost two ounces. Then, burning his plant and weighing its ashes, he found the missing two ounces. So he naturally wondered how came the plant by this enormous increment? He then could but attribute this essentially to the retention and transformation of part of the water he had been so long supplying, and before the discovery of photosynthesis (nearly a century later), this was wellnigh as far as he could go. But with the recognition of the importance of the mineral constituents, new advances as towards the science and art of manuring became possible—and are still in progress.

The student still too commonly comes to the subject, if not even with the old popular error, quite uninformed, or else is puzzled by the later taught antithesis between the typical plant and the animal which still survives too commonly. All ordinary animals take in organic food, especially proteins, carbohydrates, and fats: all fungi, from mushrooms to moulds, and the common kinds of bacteria do the same; parasitic plants such as dodder and broom-rape absorb organic food from their hosts; and insectivorous plants, like the sundew and the fly-trap, so far attain to the animal level of nutrition. Thus the student's difficulty is at once raised by the frequent statement even in textbooks, let alone in school, that the "food" of all ordinary green plants is *inorganic*, fundamentally consisting of carbon dioxide and soil-water. This again is complicated by the farmer's and gardener's way of speaking of manure as plant-food—a conception again surviving from the Roman usage—(which, indeed, actually deified manure!), and with which European agriculture is so essentially continuous, since the modern teaching of

scientific agriculture has not even yet by any means fully reached it. The famous Liebig did great service in penetrating into the inorganic chemistry of manure; so from him essentially dates the conception of chemical manures as "the ideal plant-food", and this has long been prevalent—as even up to the recent preparation of nitrates from the atmosphere. Yet again, since bacteriologists explained the Roman initiative of utilising leguminous crops for soil-enrichment in one rotation, this subject has been coming to the front in soil-science, till some of its advancing experts are breaking with what they consider the exaggerated inorganic manuring prescribed by the chemists.

The student's difficulty increases when he is told of photosynthesis, and so of the origin of "plant-food" in the green leaves by day. As teachers, we thus find our students with most or all of these ideas in serious confusion, since in unadjusted medley. We have then carefully to explain that the true food of plants consists of organic compounds which are built up in their green cells out of carbon dioxide and water, plus some mineral salts which are brought up in the rise of sap from the roots, and with their protein substances as a further outcome of this synthetic process. By this usage plants and animals are brought into line as regards nutrition.

Coming now to main particulars, the organic substances which form the daily food and seasonal reserves of plants have now long been referred to three principal classes—proteins, carbohydrates, and fats. Proteins, as already stated, form a large class of nitrogenous carbon compounds, of protean variety and intricate molecular complexity. The more complex ones include, besides carbon, hydrogen, nitrogen, and oxygen, a little sulphur and sometimes a little phosphorus, sometimes too a trace of iron as in hæmoglobin, or of copper as in the analogous hæmocyanin of many invertebrates. A very pure protein is "white of egg" or albumen; and equally familiar is the one that has been longest known for plants: the gluten of wheat grains. The formula of the albumin of white of egg has been estimated as $C_{1428}H_{2244}N_{364}O_{462}S_{14}$; but as to the actual arrangement within such molecules there is still very great uncertainty. An important consequence of the largeness and heaviness of these protein molecules is their slow, indeed all but negligible, diffusibility.

Proteins are groups of amino-acids linked together, and into these they are, through several stages, broken down in the process of digestion, only to be built up again in some other form within the living cells of the body, for all protoplasm includes proteins as the most essential of its constituents. Amino-acids, which have of late years been gaining such importance for interpretation of proteid chemistry as to have been called "the building-stones of life", may

be simply thought of as based on fatty acids in which a hydrogen atom is replaced by the amino-group NH_2. Thus, to take the simplest one of these, acetic acid, the formula is:

$$CH_3 . COOH;$$

and if one of the three hydrogen atoms in the CH_3 group is replaced by NH_2, we get:

$$CH_2(NH_2) . COOH$$

which is one of the simplest amino-acids, called glycine. Many of these amino-acids, of which there are a number of great groups, have been prepared synthetically. Many are common in plants; and aspartic acid may be mentioned as a common yet fairly complex example.

Another group of foodstuffs built up by and used by green plants are the carbohydrates, usually $C_nH_{2n}O_n$, in which n is 6, or a multiple of 6, even up to several hundred. They include sugars, a very readily transportable form of food; starches, the most conveniently storable of reserves; and celluloses, forming the walls of vegetable cells. Of each of these there are many kinds, and their chemical structure is still uncertain above the level of the simpler sugars. The simplest of all is formaldehyde, HCOH, a transient substance, probably the first to be synthesised in the green leaf, and which probably enters into the construction of many of the more complex carbohydrates.

The third group of foodstuffs that green plants make, primarily for themselves and incidentally for animals, are the fats and oils (lipoids). They are very common and familiar to us, e.g. in olive, linseed, and palm oils. They are compounds of glycerine and fatty acid, and in digestion they break down into these anew. Allied to true fats are the lecithins, very abundant in plants, and familiar, along with the protein vitellin, in the yolk of eggs. Fats form an essential constituent of protoplasm, and they play some part in determining what may or may not pass through the cell-wall.

FUNDAMENTAL SUSTENANCE OF LIFE

No ignorance of biological science can be more serious than the still prevalent failure to appreciate the life and work of the green leaves, which in their more than astronomic numbers cover all that is habitable by other life throughout the world. To realise this is an intellectual revolution, indeed one far more practically important than that from Ptolemaic to Copernican, New-Etonian to insteinian, or even from creationism to evolution. For the

photosynthesis of green leafage is the all-sustaining process of life, fundamental (with but practically trifling exceptions) to our whole living world, plant, animal, and human.

Our agriculture and horticulture have of course always depended on this process; but even our present knowledge, clear, though of course still very incomplete in its chemical and physical detail, dates only from the later eighteenth century.

We should pause here to recall some of the steps by which a general recognition of the import of photosynthesis was reached. There had been sporadic suggestions from time to time, as when Cesalpino compared the vessels of plants to veins in animals, when Helmont proved that green plants did not get all their food-materials from the soil, when Malpighi suggested that leaves elaborated the crude sap, when Mariotte compared the ascent of soil-water in the plant to the phenomena of capillarity, and so on; but the beginning of precise vegetable physiology practically dates from Stephen Hales (1677–1761), who, with a rigorous scientific mind, insisted on measurement and measurement. By ingenious experiments he "made his plants themselves speak", and besides his fundamental work on the ascent of sap, he was the first to prove up to the hilt that a great part of the food-material of green plants must be derived from the air.

The next impulse came from chemistry, which Lavoisier had begun to reorganise. In 1774 Priestley (1733–1804) had discovered or re-discovered oxygen, and five years later he showed that this gas was, in the sunlight, exhaled by green plants. In the same year Ingenhousz (1730–1799) took an even bigger stride, emphasising the facts that the oxygen was given off only by green parts and only in the sunlight; that this is quite distinct from another process (of respiration) in which plants, like animals, give off carbonic acid gas; and that the chief source of the carbon found in the carbon compounds of plants, e.g. in wood, was to be found in the carbonic acid gas of the atmosphere.

In 1800 Senebier (1742–1809) corroborated Ingenhousz's discovery of the decomposition of carbon dioxide by green plants in the light. More important, however, was the work of Théodore de Saussure (1767–1845), son of the famous explorer of the Alps, who introduced the quantitative method of estimating a plant's income and expenditure, and thereby showed that the elements of absorbed water become fixed in the plants as well as the carbon of the carbon dioxide; that respiration is as essential to plants as to animals and is related to the internal heat of some plants, as within the spathe of Cuckoo Pint and inside some flowers; that plants are unable to use the free nitrogen of the air (a conclusion now modified by the discovery of some nitrogen-fixing Bacteria and Fungi); and that there is no normal nutrition for plants apart from nitrates and other

nitrogenous salts in the soil. Such were some of the steps towards—we must still say *towards*—an understanding of photosynthesis.

How then shall we broadly outline photosynthesis? It is the utilisation of the radiant energy of red-orange-yellow light-waves, shining through the plant's green pigment which, in some subtle way, enables the living matter to build up organic carbon compounds out of carbon dioxide and water. In ordinary land-plants the water is absorbed by the roots, and in submerged plants over the whole surface, but it also can be taken in by exposed aërial parts, as by the delicate surfaces of liverworts and mosses, and in the perched plants (epiphytes) that have no contact with the ground. The carbon dioxide may enter along with the water, either in simple solution or in loose chemical union (H_2CO_3). Soil-water also contains small quantities of mineral salts, which have their necessary and subtle rôle.

The laboratories in which the photosynthesis takes place are the "chlorophyll grains", small protoplasmic corpuscles or discs, containing this green colouring matter, and technically called chloroplasts. They are semi-solid differentiations of the cytoplasm in which they lie, but have been often described as multiplying by division. In most higher plants they have a bun-like shape, which may be modified as their position within the cell is adjusted to light and gravity. In some of the Algæ they have rather striking shapes, sometimes like stars. They are tinged by a complex of chlorophyll pigments—which are discussed in another section. In brief, there seem to be usually two "chlorophyll-greens" which are essential, and two "chlorophyll-yellows" which are ancillary.

The energy utilised in the photosynthetic process is that of the red-orange-yellow light-waves which are absorbed by the chlorophyll-complex. The light is essential, for a green leaf cannot make carbohydrates in the dark; and the chlorophyll is essential, for the carbohydrates are only formed in the chloroplasts. What exactly takes place is still unsettled among the biochemists, but it seems probable that "the light is changed into electricity"—i.e. to wave-lengths in another octave of the long gamut of electromagnetic radiations or ether-waves. It is also probable that this electric energy reduces the carbonic acid (H_2CO_3) first to formic acid and then to formaldehyde (H_2CO), which is then compounded into more complex carbohydrates, e.g. glucose (grape sugar) and saccharose (cane sugar). In the reduction process oxygen is given off as a by-product. It seems that only a small percentage, 0·5 to 3, of the energy absorbed by the chlorophyll is used in photosynthesis: part of it goes to warm the interior of the leaf, and thus to help in the vaporisation of water—a very important process. The green plant's power of changing the radiant energy of light into the potential energy of carbon compounds commands our admiration, but it

must be admitted that the leaf remains far from ideally efficient when we consider the relation of the energy absorbed to the amount of work done. In fact this limited productivity inspired the great chemist, Berthelot, to predict a Utopia, in which the chemical factory should replace the field!

As to the products formed in the chloroplast laboratories, sugar and starches are among the first stable substances to appear, probably, as we have said, through the intermediation of formaldehyde. But there are many plants in which starch is not formed at all, or only in exceptional conditions. Instead of starch there may be oil, or it may be that the simpler carbohydrates are diverted from the path leading to starch formation to one which leads to amino-acids or other nitrogenous compounds.

As all living matter includes protein substances, the most abundant and probably the most important of its constituents, we must continue our outline-inquiry a step further, and ask how the plant makes its protein food. Since proteins are nitrogenous carbon-compounds, whose molecules often include some sulphur atoms, and in many cases some phosphorus as well, it is evident that they cannot simply be built up from carbohydrates. The question is the source of the nitrogen, and the first most obvious *a priori* answer was—the atmosphere; for this contains 78 per cent. of the element required, and is present in the endless air-spaces of the soil, and dissolved in the soil-water, and so in the sap that ascends and transpires. Yet there is no evidence that any plants, save certain fungi and bacteria, and the leguminous plants (with a few others) with which these bacteria have formed a root-symbiosis, can utilise free nitrogen.

For ordinary plants, and not entirely excluding those with symbions, the saprophytes, the parasites, and still less the insectivorous species, which after all grow normally in the main, the essential source of nitrogen is by way of ordinary root-action which brings up the nitrates of the soil; and these are mainly traceable to organic matter decomposed by microbes. These nitrate salts are carried in the sap to the living cells of the plant, and in the presence of unstable or nascent carbohydrates, are built up into proteins.

Though our knowledge is still very insufficient, it seems reasonable to regard the upbuilding of proteins as a climax of the anabolic and synthetic processes which occur in the green leaf. Starting from its synthesis of carbohydrates: these may be converted into amino-acids by the reduction of the sap nitrates to ammonia, and these amino-acids, by linkages with others and by incorporation of sulphur and phosphorus molecules from the sulphates and phosphates also in sap-solution, may build up proteins. But along this line of inquiry there is as yet more of scientific imagination and endeavour than settled result.

Before passing from the photosynthesis in Nature to Professor Baly's artificial photosynthesis, we must emphasise the ecological importance of the ordinary world process. In short then, (*a*) it is on this activity of green plants that they, and the animal world from them, depend directly or indirectly for sustenance; (*b*) the liberation of oxygen as a by-product has been gradually—and this throughout geologic time since verdure began in sea and on land—evolving a breathable atmosphere, needed even for plants themselves, and for animals yet more; (*c*) the formation of carbon compounds has led to the accumulation of the potential energy of coal-beds, lignites, and peat-mosses: and as we consume these CO_2 is returned to the atmosphere. Yet far more has been locked up, and mostly by animal life, in static and practically irredeemable form, in the limestones and chalk which bulk so largely in world geology.

Baly's Artificial Photosynthesis.—Professor Baly, of Liverpool University, and his collaborators have been able to imitate (if not in some measure also reproduce) the photosynthesis that occurs in the green leaf. Water containing carbonic acid was subjected to prolonged illumination by a mercury-vapour lamp (giving out light with very short wave-lengths), and the result was the appearance of formaldehyde (CH_2O), which many botanical physiologists had come to regard as the first or second carbon compound to be built up in the leaf. With continued illumination of the solution with light of somewhat longer wave-length, he obtained glucose, which is one of the main products of natural photosynthesis.

Still with the mercury-vapour lamp, Baly proceeded to induce the formaldehyde to unite with nitrites, thus forming nitrogenous carbon compounds; thus approaching the proteins which are characteristic of living matter. It will be noted that nitrites are substances readily available in Nature, being produced for instance when lightning fixes the nitrogen of the air in the form of nitrous oxide, which is brought down by the rain in the form of nitrite of ammonia. Chemical industry now does something closely analogous in fixing the free nitrogen of the air by help of powerful electric discharges, and thus obtains a basis for the manufacture of nitrogenous fertilisers.

Meeting the objection that we do not quite find the equivalent of the mercury-vapour lamp in nature, Baly next devised a further photosynthetic process, less artificial, since using ordinary sunlight. In the presence of certain "photo-catalysts", that is to say coloured substances which make the energy of the light more available, the same substances were formed again. An encouraging result; yet to which the previous objection reappears, against the use of an artificial catalyst. Yet to this may be answered that chlorophyll as an iron-containing pigment, may be, or may contain, the catalyst.

These highly interesting experiments require to be confirmed and

extended, but Baly has apparently approached the confines of living matter without using any material or means not readily available in Nature. With the help of light he synthesised nitrogenous carbon compounds from carbon dioxide and water and nitrites. May not all this be at least peeping through a chink in the door which has so far shut out from us the mystery of abiogenesis?

The twofold story—of diminishing carbon dioxide and increasing oxygen—is thus nothing short of that of the evolution of the atmosphere. This did not escape the speculative mind of Kelvin half a century ago or more; but it does not seem to have been carried much further. Geology, in its widest aspects, has of course almost from its beginnings been considering not only the earth's solid crust, and this as early formed upon a cooling but still unsettled world, but also the significance of its waters, and in their circulation from oceans and seas, and of their evaporating and condensing water-vapour by rain, whence rivers, and these denuding and sculpturing the older rocks as they descend, so ever laying down new strata in the sea, and towards their varied upheavals. But the earlier question is that of the withdrawal of oxygen from the primitive atmosphere of our planet, as by its union not only with most of the available hydrogen as water, H_2O, and with carbon for CO_2; and, above all, by its formation of the primitive crust, by union with the accessible metals, which earth-weighing experiments have long shown to have been predominant in its mass from its beginnings. When the world was thus crusted over, and thence superficially cooled, enough for the precipitation of water-vapour, the oceans would arise; hence leaving an atmosphere mostly of passive nitrogen, with much carbon dioxide and water-vapour, but with little oxygen left uncombined. Here, then, were conditions more favourable for the beginnings of plant-life than for animal, and this presumably aquatic, but in simpler forms than any we know or can imagine; yet with increasing contribution of oxygen as its waste-product. With this enrichment of the atmosphere in oxygen, animal-life could not but be aided and intensified—so on such long-continued lines of atmospheric changes can we avoid seeing a dual action on life in its evolution? It has often been pointed out that the exuberant vegetation which has given us our coal-beds suggests a moist atmosphere, rich in CO_2. Yet the objection arises—why not coal in earlier strata? since even by Carboniferous times life was immemorially old, and something of moist land conditions must surely have existed long before that period. Here, as so often, the imperfection of the geological record still baffles us (though graphite deposits may be thus explained); yet all the more such questions must be kept in view. The vivid and well-argued hypothesis of René Quinton—that the lower specific gravity of the fluids of land animals, as compared with sea-water (which is, of

course, ever saltening from its incoming rivers), may correspond to the time of their emergence from the sea—may here be suggestive. For can the somewhat kindred speculation be avoided, that the gradual extinction of old forms, and the appearance of new types, and these respectively of plant and animal life, may have been influenced by these atmospheric changes? No doubt the persistence of a good many ancient types in both kingdoms seems an objection; yet may not these be but survivors through a little more respiratory adaptiveness? Difficult though this problem be, experiment has long shown the advantage to vegetative growth through considerable increases of CO_2, and experimental embryologists are applying both kindred and converse atmospheric changes to animal-life also; so why not continue such questionings, and see if in time we can interpret them more widely?

THE TRANSPIRATION CURRENT.—How far we would travel to see water rising high into the air and then falling in green spray. Yet few of us have to travel far; for, as Ruskin long ago said, the tree is a green fountain, and with the further marvel that its waters do not fall. The birches and beeches, the horse-chestnuts and sycamores, the larches and all the wood—what assemblage of life's fountains! There is no doubt that water has to rise to the topmost branches of these lofty trees and even to three or four hundred feet in the great Australian eucalyptus, if the buds of last year's making are to be unfolded. No doubt some water is stored in the stem of the tree, but that serves only for a beginning; the bulk of the water has to be raised out of the soil. How is this done? Moreover, apart from the swelling of cells that bursts the imprisoning bud-scales, there is the rapid growth of the potential leaves, which spread themselves out to the sunshine. Everywhere in growing tissue there is the intricate process of cell-division—in its way more wonderful than the making of a double star. All the new cells have to be fed, and this means making abundant carbohydrates and proteins, and so forth. In other words, there has to be photosynthesis.

Living matter or protoplasm contains at least seventy-five per cent. of water, so that its growth and increase demand much water. The food-making photosynthesis also requires water as one of its raw materials. Whenever the growing leaves expand in the genial air there is not only evaporation, but active transpiration, and this is the largest demand of all. Hence, then, it is that the fountain does not fall.

Everyone who knows the whistle that the herdboy made knows how easy it is, with moistenings and tappings, to slip off the rind of a three-inch piece of a young branch. The rind slips off from the wood by the ready rupture of the "cambium layer", yielding and

viscid, to the touch because of its embryonic and dividing cells. The white wood is thus exposed, with its youngest "sap-wood" outermost: so called because it is here that the water ascends. The "bark" which slips off for our whistle has its own complexity, with soft bast and its living cells and sieve-tubes, and its hard bast with its tough and flexible fibres (so often important to man), while outside this there is in young shoots a layer of green parenchyma and an epidermis, much as in a leaf. In stems that have to stand the winter a cork layer appears, with uniquely developed characters of impermeability to water, and of non-conducting defence against both heat and cold—qualities hence again eagerly utilised by man.

But now let us concentrate on this young wood. It consists of elongated spindle-shaped cells (tracheids), and also of vessels (tracheæ), formed from the end-to-end fusion of cells; and both these kinds of elements have thinner spaces in their substantial walls, through which water may pass laterally. The strands of the young wood form the path for the so-called "transpiration current", or, in other words, for the ascent of watery sap; and some investigators maintain that they also serve for sugary sap passing downwards; and not the soft bast alone, as was formerly believed. If we may compare a plant with an animal (though this is always dangerous, this young wood may be likened to the blood-vessels. Or, dropping the comparison with animals, the young wood is the main transport system. The fundamental fact is that these wood-strands form a continuous system extending from just below the absorbent root-hair region of every rootlet to the central framework of the leaf. Every cell of the root-hair region and every cell of the central tissue of the leaf is in close contiguity to a wood-strand—to the young wood elements of a fibro-vascular bundle. Thus there is a living and working continuity from the place where soil water is captured to the place where carbon compounds are synthesised. Yet what positive proof is there that the young wood is the ascending pathway for the watery sap?

There is a general correlation, suggestive if not convincing, that high-climbing plants with narrow stems show strong development of wood-strands, while submerged aquatic plants show a very poor development of this tissue. But more conclusive evidence is afforded by girdling and cutting experiments, which show that removal of the bast is not followed by wilting, whereas cutting the young wood is at once followed by the wilting and probably by the death of the leaves. More precise experiments, utilising some readily recognisable injection material, such as Chinese ink, have proved that the main pathway of the ascending water is by the young wood-vessels or tracheæ. The fluid can be seen passing up these microscopic pipes, "swirling into their open ends", as one botanist puts it. The neat converse experiment has been made of plugging

the vessels with melted paraffin or gelatine, which solidifies when it cools. In such cases the leaves of the shoot soon wilt. While one must not conclude that no water can pass up in the walls of the vessels, the main path is certainly in the cavities themselves.

ASCENT OF SAP.—The essential question is—how does the water rise, against gravity, and to the tree-top?—a height which even in ordinary trees so much exceeds one or two full pump-lifts, and in really lofty ones a good many more, even to the equivalent of ten or even a dozen atmospheres? Many answers have been suggested, but we cannot here go into all these. Indeed, it would need a volume to do them full justice, since ranging through two centuries of speculation and investigation, as from Hales to Bose, and even onwards. Witness the former's root-pressure theory, the atmospheric-pressure theory, the capillarity theory, the "relay-cells" theory, and so on, to Bose's recent intra-cellular pulsation-lift theory, as we may call it; each of which has been ably argued for, and more or less experimentally supported as well. Return, then, to look once more into the essential phenomenon, which each and every theory has sought to explain: That—not simply by passive evaporation, but by active transpiration—much water passes off from the leaves as water-vapour; so to keep up this vast expenditure is the fundamental condition necessitating the corresponding ascent of sap. And since the wood-fibres and wood-vessels form a series continuous from root-points to leaf-tips, we have thus to visualise what are practically long water-columns, albeit in more or less transverse continuity also. But for familiar physical reasons, these columns are very hard to break, though easy to bend, so that as Herbert Spencer pointed out long ago (another theory!) the very swaying of the wind, instead of hindering, must more or less help them onwards. The leaf-cells, transpiring so much water, must needs replace this from the water-column in the closely adjacent wood-fibres and vessels of the leaf; and so they cannot but be exerting a potent pull upon the whole water-column below. They thus contribute to its rise; but in what measure? Were this pull of the leaf-cells merely a question of ordinary hydrodynamics, it would not suffice beyond a single atmosphere or pump-lift: but—here another contribution—these living cells of the leaf-parenchyma and epidermis have their osmotic properties modified by their work of transpiration, and thus with their pull potently increased upon the coherent water-columns below. Here, then, is the old *vis a fronte*, now developed as "the cohesion-theory", as its foremost exponent, Prof. Dixon calls it. To our minds this seems at least the central and elemental interpretation, since osmotic pressures may rise to not a few atmospheres, as most physiologists seem coming to agree. Yet none the less—even as for Spencer's minor contribution above

cited—each and every other theory must still be taken into account. Thus Hales' initial and classic experiment, showing the rapid up-pushing of water from a vine-stock cut so close as to have no leaves at all, demonstrates the existence of his *vis a tergo*, especially, of course, in the early growing season, when leaf-buds are thus being helped (indeed forced) to open. Moreover, this root-push loses its mystery, when we find in it the osmotic pressure produced by the transformation of its insoluble reserves to plant-food in solution.

In such ways, then, each of the many ascent-theories has to be reckoned with, and for all that it may be worth; and, indeed, who can say that no further factor of ascent may still remain to be disclosed? Even the descent of sugary sap, though small in quantity and apparently slow also, as compared with the enormous and rapid ascent of watery-sap, must also be recognised as a minor and indirect contribution towards necessitating the ascending current. And thus so far it extenuates the failure of Hales' initial theory (induced by mistaken analogy from Harvey's proof of the circulation of the blood), and surviving to this day in popular language—as out-of-date scientific theories so often do—as "the circulation of the sap", though "the ascent of sap" has long been seen as the essential process, and problem.

In such ways, then, we see the necessity and the promise of continued investigations, and these more and more comprehensive; since needing to be pursued into the analysis and comparison of sap-movements in all kinds of vegetation, from simple to complex, small to great, and in all their life-phases; and these again throughout the changes of day and night, of temperature and pressure, of season and climate, and of material environment—in all their aspects, favourable or hostile. Much towards this has, indeed, already been done, but necessarily as yet too sporadically. Revision and co-ordination, as in so many other fields, are here needed before we can understand sap-movements as comprehensively as physiologists and physicians have been mastering their problem of the circulation of the blood. In this progressing synthesis—doubtless calling for the co-operation of many laboratories in many lands—the various special viewpoints and theories will find due place; and this doubtless in varying proportion, as with that of Hales for the vine's growth-season. Our successors will thus at length be able to admire this varied and varying play of Nature's green fountains with clear intellectual conscience, and throughout all her enchanted woods over the wide sunlit world.

Transport of Foodstuffs.—In a typical plant the transpiration current or "the ascent of sap" is obviously necessary to bring the food-materials of water and salts, and dissolved carbon dioxide as well, to the seat of photosynthesis, which in most cases is in the green leaf. The question now arises: how the carbohydrates

fats, and proteins are transported from the green working cells, through the plant, to feed its other cells, to afford material for immediate growth, or to be stored for subsequent use.

If the food is to pass from the place of manufacture to the place of usage or storage, it must be able to diffuse through living cells, and this must often involve a change into a state suitable for translocation. Thus cane sugar($C_{12}H_{22}O_{11}$) probably travels as some simpler sugar, such as glucose ($C_6H_{12}O_6$); fats travel as fatty acids and glycerine, just as in our own body; and proteins probably travel as amino-acids. The change into a diffusible or travelling form is brought about by ferments to which we shall refer later on.

In a simple plant like a seaweed or a liverwort, the food passes by osmosis from cell to cell, often helped by the bridges of protoplasm which penetrate the cell walls; but in higher plants there are special paths which effect more rapid transport. The usual view of botanists is that this conducting system is mainly to be found in the soft bast, helped sometimes by the vessels which carry the milky material called latex, so familiar in spurges and dandelions, and so important to us in rubber plants.

In seed-plants the phloem or bast strands lie to the outside of the xylem or wood-strands, and except in monocotyledons the two systems are separated (should we rather say *united?*) by the cambium zone of persistently embryonic cells, rejuvenescing and dividing with each growing season. Like the xylem, the phloem forms a continuous system from the stem to the roots below, and to the leaves above: thus it is easy and interesting to tear them apart from a fallen and slightly decayed holly leaf, this yielding two exactly similar half-skeletons. Yet in some cases, at least, they do not usually extend quite so far as the xylem into leaf and root points, since the exit and entrance of water is the more urgent. Then, too, as the wood and bast of any stem so plainly shows, as do also our leaf half-skeletons aforesaid, the wood breaks readily, while the bast fibres only bend, and thus the stem and branches are stayed, essentially as the masts and spars of our ships by the rope-rigging—which wood and bast-fibres have respectively supplied us. This mechanical combination and perfection of the leaf-skeleton, however, incomparably surpasses man's rough skill.

We are not in this sketch concerned with any full account of the various elements that make up the phloem strands; but outstanding amongst them are the "sieve-tubes"—living vessels formed from the fusion of the end-walls of a line of cells, and yet with their protoplasm in continuity through perforated-looking septa, of characteristic aspect. They are thus not fully comparable to the tracheæ or wood-vessels of the xylem, which lose their protoplasm and which certainly carry water, and so have usually been regarded as the main transport-lines for the food, especially in its descent from the

leaves. But just as the tracheæ, or wood-vessels, are aided by the tracheid cells, the wood-fibres, so the sieve-tubes of the phloem have "companion cells" and "bast-parenchyma", often compared to side-lines of transport.

Many reasons have been given for regarding these complex phloem strands as the conducting tissue for the synthetised foodstuffs in solution, the "elaborated sap", as it used to be called. The observations show that the pith and the outer bark may be left out of account as quite unessential for transport; the outer and younge-wood-layers seem preoccupied with the transpiration current; while experiments show that a cutting or blocking of the phloem strands stops, or at least retards, the translocation of foodstuffs. Moreover, a biochemical analysis of the coagulable and colloidal contents of the sieve-tubes shows that they are peculiarly rich in soluble foodstuffs, or, to be cautious, in complex carbon compounds. This is also true of the contents of the latex vessels, whose milky contents yield us opium, india-rubber, and gutta-percha, and thus seem more suggestive of storage (if not sometimes also of riddance) than of transport. An indirect argument in confirmation of the view that the phloem strands form the main food-conducting system is the fact that their development is exaggerated in cases where the requirements for speedy transport are greatest, as in the stems of vines extending for many yards, and in other prolonged shoots of copious inflorescence.

But while these and other arguments support this view, very widely held, that the "elaborated sap" passes down the stem or branch by the soft bast, and by its sieve-tubes especially, the recent experiments of Prof. Henry Dixon and others point in another direction: There seems to be more than the familiar up-current in the strands of the young wood; for now these able investigators give experimental evidence of a down-current in the wood, transporting organic substances from the leaves. It is not denied that materials may pass inwards from the phloem strands, and that some of these pass into the ascending transpiration stream of the wood; yet this seems to have its down-streams also; and there is growing evidence that the materials thus borne down include hormones—perhaps growth-controlling and metabolism-regulating—besides ferments, which keep the wood-vessels in good working order, as by rendering any starch-blockage soluble.

STORAGE OF RESERVES.—It is characteristic of organisms that they "accumulate energy acceleratively", as Joly many years ago put it in his famous paper on "The Abundance of Life". A growing leaf utilises part of the previously elaborated food before it can go to work itself, and even has to make the first charge on its own product of photosynthesis, but its increase of surface makes

further efficiency possible, and this continues cumulatively till the limit of growth is reached. As a tree grows older, it enlarges its leafage area at a ratio far beyond its actual needs for growth and repair. This organic momentum—a veritable growth by compound interest, and thus rewarding afforestation—is the condition for storage, which is so characteristic of plants. Moreover, as contrasted with animals, plants do not oxidise much of their daily nutritive gain as a source of energy for work. The vital expenditures in animals tend to come much nearer their nutritive income. Furthermore, the processes of anabolism tend to increase the size of the thus elaborated molecules; and a *general* result of this is in the direction of reducing mobility. Hence the abundance of reserve-products in plants—a fortunate fact for man and beast alike.

There are not many cases of ordinary leaves becoming laden with reserves, partly because this would encumber the photosynthetic and other actively anabolic processes, and also because most leaves are organs with a limited length of life. Or, stating the fact less teleologically, we may say that the presence of diastatic and other ferments in the green leaf secures the mobilisation of starch and other synthetic products. Stores are accumulated at some distance from the seat of manufacture, e.g. in roots (as in carrots), in spreading underground stems or rhizomes (as in bracken), in compacted portions of underground stem (as in potato tubers and crocus corms), in subterranean buds (as in crucifers), in pith (as in sago palms), and notably in seeds. A process of fermentation or digestion is needed to precede the transport from leaf to store, as when starch becomes sugar, and also for the re-mobilisation of the reserves after a resting phase. The forms taken by the stored food are very varied, and several different forms may occur in one and the same plant. Commonest of all are the starches which arise, from glucose and the like, as characteristic grains in the interior of minute leucoplasts. In the tubers of potatoes, about 80 per cent. of the dry weight consists of starch; in seeds of rice and wheat, 68 per cent.; in peas, 52 per cent.; yet in almonds, only 8 per cent. Less complex than starch, and arising from fructose, is inulin, which occurs dissolved in the sap of storage-cells, as in dahlia tubers. The commonest storage form of the sugars is saccharose or cane sugar, as in grasses, of which sugar cane is but the extreme instance. Remarkable for their solidity and durability are the hemi-celluloses that are deposited inside the cell walls of some seeds, cotyledons, etc., e.g. in date-stones and coffee-beans. Yet these, too, are fermented before germination into the readily transformable sugars known as mannose and galactose.

Fats and oils are very common reserve stuffs, especially in seeds (e.g. cotton and flax), and usually occur as droplets in the cytoplasm. Proteins in solution may lie in reserve in the cytoplasm of

the cell, or may become compacted into grains, as in beans and wheat. Storage of proteins is almost unknown in animals. Amino-acids are exceedingly common in plant stores, usually along with other reserves. A rare but interesting condition is illustrated by some condensed alkaloids, such as those of "cocoa" and coffee.

We have so far thought of most if not all the alkaloids and kindred complex products, such as thein or caffein, etc., as put out of the plant's way, like the oxalic acid crystals of a rhubarb leaf, rather than as stores proper. Yet a strong argument has been brought for also considering at least the above named in the simpler way, as not without more or less reserve value.

It is probable that the complex milk or latex (at once solution, emulsion, and suspension) of poppies, india-rubber tree, etc., is also in part at least of storage value.

DIGESTION.—From storage it is convenient to pass to digestion, the fermentation which changes the reserve material into mobile form suitable for transport. Just as in animals, the food is made soluble; and that means the splitting of a complex molecule into two or more simpler ones, often with the incorporation of water. Thus cane sugar, when digested in the plant, is changed into glucose and fructose; and starch first into maltose, and then into glucose. Though plants have no special digestive cavity, the process is fundamentally the same, and is accomplished by ferments or enzymes (see Fermentation). It is important to note that some enzymes can work both ways, building up as well as breaking down; thus starch may be formed from glucose, cane sugar from grape sugar and fruit sugar, and proteins from amino-acids. As typical examples of digestive ferments in plants, may be mentioned three which are familiar in animals also: the diastase that changes starch into sugar, the lipase that changes fats into fatty acids and glycerine, and the peptic and tryptic enzymes which break down proteins. The assimilation of these by the protoplasm of the plant-cell seems much as in the animal.

RESPIRATION.—If numerous sprouting seeds or opening flowers are crowded into a corked jar, the air becomes in a few hours laden with carbon dioxide. This is at once shown by the familiar tests of the extinction of a lighted taper thrust into the jar, or by the rapid clouding of lime-water shaken up in the fouled air. Between the still living plants and the air in the jar there has been an exchange of gases; oxygen is absorbed and carbon dioxide is given off. This significant fact in the function of respiration has too much been taken for the whole process, but that has been shown to be a too superficial conception.

That respiration means more than exchange of gases is evident

when we think of anaërobic bacteria which do not flourish in ordinary air, where the free oxygen is fatal to them, but can only flourish when it is excluded. And what is true of these microbes is so far true of many tissues or even entire multicellular organisms normally aërobic; that if oxygen be excluded they may continue living anaërobically for a considerable time.

In animals that breathe dry air, say mammals, there are familiar arrangements which secure the inhalation and exhalation of air from the lungs; and the out-breathed air has less oxygen and more carbon dioxide than the in-breathed air. In our ordinary talk we speak of the inhaling and exhaling as the breathing or respiration; but the real function of respiration is a much deeper process—namely the oxidation that is associated with the energy-changes that go on in the living matter. Oxygen, brought to the tissues and cells, is utilised in the breaking down or katabolism of the protoplasm, and the energy set free is used in various ways, e.g. in movement and in doing work. This is *the essential function of respiration*, which is sometimes distinguished, as *internal* respiration, from the arrangements for capturing oxygen and getting rid of the poisonous carbon dioxide, which are summed up in the term *external* respiration. These arrangements are very diverse in different types of animals, some using gills and others lungs, some using air-tubes and others the skin; but the gist of internal respiration is always the same except in anaërobic organisms.

Similarly among plants, a distinction is usefully drawn between the aerating system, e.g. the interspaces and channels in the under part of the leaf, and the internal respiration which concerns the breaking down of the protoplasm or of complex proteins associated therewith. The air enters and leaves ordinary flowering plants by the minute openings or stomata, most abundant on the under surface of the leaf, but there is also diffusion in and out through the delicate epidermis, apart from any openings.

But the gaseous exchange involved in aëration (corresponding to the animal's *external* respiration) is to be distinguished from the release of energy by the breaking down of complex carbon compounds which form part of or are closely associated with the protoplasm (corresponding to the animal's *internal* respiration). In some plants part of the energy released takes the form of heat, but this is not known to be of use in the plant; and the same may be said perhaps of the lower animals, in which it is not conserved and accumulated as in birds and mammals. In these warm-blooded organisms the animal heat, automatically kept at a constant temperature, is quantitatively sufficient to have an important rôle in increasing the rapidity of chemical reactions and securing a smooth-working metabolism. In plants the rôle of the oxygen in the internal respiration is essential to growth and to activity, and one of the

ways in which it works is probably in removing substances whose accumulation would interfere with continued growth and activity. The final results of the breaking down are CO_2 and H_2O; but it is characteristic of the very economical metabolism of plants that early stages in the breaking down of complex molecules may be arrested and rebuilt into proteins again.

At one of the early meetings of the Royal Society, in 1667, Robert Hooke produced experimental evidence to show that in certain circumstances a dog would die because of "the want of a sufficient supply of fresh air". Soon afterwards (1674) John Mayow recognised that there was in the atmosphere a particular constituent (*spiritus nitro-aereus*), which was indispensable for the continuance of vital activity *and* for ordinary combustion. "Animals and fire draw particles of the same kind from the air." "With respect, then, to the use of respiration, it may be affirmed that an aërial something, whatever it may be, essential to life, passes into the mass of the blood. And thus air driven out of the lungs, these vital particles having been drained from it, is no longer fit for breathing again." The *spiritus nitro-aereus*, the "vital particles", the "aërial something", must be identified with what we call oxygen, which was again discovered (after Mayow) by Priestley in 1774, who also showed that air "spoilt" by animal respiration may be restored by the activity of green plants in the sunlight. But Priestley's rediscovery of oxygen, which he called "dephlogisticated air", was wrapped up with the erroneous "phlogiston" doctrine, that burning meant the liberation of a special compound, phlogiston or fire-stuff. Thus it was reserved for Lavoisier, a little later, to explain the real nature of oxidation, and to bring into line the burning candle, the living animal, and the plant as well, the last being studied at night when photosynthesis is in abeyance. In all three cases, oxygen from the air is uniting, directly or indirectly, with the carbon of carbon compounds, and forming an oxide of carbon (CO_2) which Black had discovered in 1755 and called "fixed air". Yet the student must seek to avoid the false simplicity of identifying internal respiration and combustion; for not only does the respiratory reaction in the living cells go on at a low temperature, but it is very unlikely that the oxygen rushes directly into union with the carbon of carbon compounds. The "fire of life" is subtler than that of the hearth.

Thus as regards plants there is reason to believe (1) that a carbon compound, especially a carbohydrate, may be split, *apart from the action of oxygen*, into carbon dioxide and a readily oxidised substance; and (2) that the latter, *by the action of oxygen*, may then undergo combustion. It is also held by some physiological botanists that a distinction must be drawn between the breaking down of a food-substance like sugar, comparable to fuel, and the more fundamental breaking down in the protoplasm itself.

LIFE WITHOUT OXYGEN.—Pasteur discovered that some moulds and bacteria could live without free oxygen, and he called this mode of life anaërobic. In the presence of oxygen, the yeast plant feeds on glucose and multiplies rapidly, forming carbon dioxide and water. In the absence of oxygen the yeast plant ceases to grow or multiply, but it ferments the sugar into alcohol and carbon dioxide, producing heat in the process. At some stage, oxygen must be formed which unites with part of the carbon of the glucose to make carbon dioxide, some energy being released for the plant's use, but in a somewhat wasteful way. Some bacteria are killed, as Pasteur showed, by oxygen; and it is noteworthy that the chemical results brought about by putrefactive organisms differ greatly according to the presence or absence of oxygen. In general it may be said that the anaërobic respiration does not carry the breaking down of the proteins so far as to the usual carbon dioxide and water, and does not liberate enough energy to admit of growth.

It is convenient to refer here to cases of "anaërobiosis" (life without oxygen) in the animal kingdom. In experimental conditions some animals, e.g. leeches, remain alive for over a week without any oxygen; and in natural conditions they can live with a very scanty allowance. Thus there is very little oxygen in the depths of many sluggish lakes, especially when they are frozen at the surface; yet freshwater mussels survive these conditions, passing into a lethargic state at the unfavourable season. Spallanzani showed that snails can survive for some time in an atmosphere of nitrogen or hydrogen; and it is said that they continue to give off carbon dioxide in these conditions.

Experiments on muscle are very instructive in this connection, for when stimulated in the absence of oxygen it gives off (for a short time) the usual lactic acid, which remains as such, while in the presence of oxygen the lactic acid is partly oxidised, with the production of carbon dioxide. Thus the end-product is different according as the process is anaërobic or aërobic.

Many Nematode parasites spend the greater part of their life within the intestine of higher animals, surrounded by the partly digested food—from which they exact a toll—and the other contents of the alimentary canal. Now this medium, as Bunge showed long ago, contains almost no oxygen. In some cases no trace of oxygen can be detected, yet the worms produce carbon dioxide. In solution of this puzzle, it has been suggested that the worms bring about in their body a fermentative process, which supplies the energy needed for movement, growth, and other activities. It may be that the fermentation of glycogen, abundantly stored in the worms, yields in the absence of oxygen valerianic acid, carbon dioxide, and water, and releases energy as the rather abnormal yeast plant does in its fermentation of sugar into alcohol.

Some recent work on parasitic worms has, however, raised again the doubt whether they are so really anaërobic as they seem to be. Thus Slater, working on Nematodes, has shown experimentally that the worms do not thrive in the absence of oxygen—they have merely great endurance; it follows that they must normally get oxygen from somewhere, and most probably from the blood of the host. It has been shown that dyes dissolved in the blood of the host may find their way into the tissues of the parasite, and it is likely that oxygen may be transported in a similar way. All this makes it seem doubtful whether any animals can survive absence of oxygen except by passive resistance.

MOVEMENTS OF PLANTS

Some of the simplest plants, as among the unicellular or few-celled Algæ, have flagella or lashes of living matter, by means of which they propel themselves through the water. One of the phases in the life-history of the Slime Fungi, if they are regarded as plants, is flagellate; and it is succeeded by a less active, but also motile, amœboid phase. Many bacteria move rapidly by means of numerous cilia. The threadlike Oscillarias, consisting of a single row of cells, are able to sway about in the water and to creep along a substratum—an early instance of the co-operative activity of cells. The flinty-shelled diatoms, which form a very important part of the microscopic plankton—the food of many pelagic animals, move about in a somewhat puzzling way, probably by the emission of very delicate protoplasmic threads. Many spores among the lower plants are actively mobile in water, and sperm-cells with cilia or flagella occur not only in ferns and mosses and their relatives, but as high up in the scale as Cycads and Maiden's Hair trees. More fam liar are the movements of climbing plants and of some of the insectivorous forms like the sundew.

But even when all the many cases of plant movement are considered, the well-justified impression remains, that plants are characteristically different from animals in expending relatively little energy in locomotion or external work. They use most of their energy in growth and in internal work. It is just saying the same thing in another way if we emphasise the fact that the ratio of constructive or anabolic processes to disruptive or katabolic processes is always much greater in a green plant than in an animal of about the same size and weight $\left(\frac{A}{K}\text{ much greater than }\frac{a}{k}\right)$. A consequence, which also helps as a cause, is the enclosing of the plant-cell in a wall of cellulose, which must greatly hinder mobility. There are often streaming movements within a cell, and diffusion move-

ments from cell to cell, but the larger movements of parts, which are so conspicuous when animals move their appendages, are inconspicuous and slow in plants. In his highly educative *Botany of the Living Plant*, Prof. Bower states the case vividly: "One reason for their slowness is no doubt the fact that the protoplast of each cell, though it is the vital agent, is not so free to move as are the protoplasts of the animal body: for it is encysted by its cell wall. Like the mediæval knight, its movements are checked by its protective armour. The plant has sacrificed mobility for mechanical defence." But we must go further back and note that the initial feature, which even accounts for the protective armour, is the plant's characteristically preponderant anabolism, and this is bound up with the ability to make food out of very simple chemical materials.

Growth and Movement.—It is useful to make the contrast that the energy released in the animal body is largely utilised in movement and external work, whereas the energy released in the plant body is largely utilised in growth and internal work. But this must be supplemented by the fact that the movements of plants, such as they are, cannot *in the majority of cases* be separated from growth. In other words, plant movements are commonest in parts that are still young and growing, whereas the most striking movements of animals, such as the flight of birds and insects, are exhibited by finished structures. We shall begin our brief survey, then, by referring to the growth-movements of shoots and roots and the like.

Nutation.—Along a plant's axis (root and stem) there is inequality of growth at different regions, and the same is seen *around* the axis in different segments. But the area of most rapid growth shifts, either spontaneously or under known stimulus, from one radial segment to another, and this is expressed in that bending and bowing to different points of the compass which is called nutation. It is exhibited by the free-growing tips of stems and roots, which describe, at varied rates, irregular circles or ellipses or spirals.

Similarly a young leaf in the bud grows more rapidly on its outer (future under) surface, and this presses it inwards against the young shoot. Later on, the more rapid growth is on the inner (future upper) surface, and this presses the leaf outwards. In short, the movements and foldings of young leaves within the bud, and the movements and unfoldings as the bud opens, are familiar diverse expressions of differential growth.

Tropisms. — Some growth-movements have their direction determined by the direction of the incident stimulus, and to these the term tropism is applied. They are obligatory movements whose direction is defined by the stimulus. Thus stems grow in a direction opposite to that of the gravity pull, while roots grow towards the centre of the earth—a familiar fact expressed technically by attributing negative geotropism to the stem and positive geotropism to the

root. How the gravitational pull makes itself felt is a problem still under discussion and experimentation, but there is much to be said for attaching importance to a change in the position of minute bodies, such as starch grains, floating freely in the cell-fluid, but tending, because heavier, to sink to the lower side. If some change occurs in the direction of the gravitational pull, the grains will come to rest on a part of the cell unaccustomed to them. This may provoke a new direction of growth-movement, the changed curvature restoring the old position of equilibrium. In almost all geotropic organs there are these freely moving starch grains. As they seem to bear a close analogy to the particles in the balancing ears of many animals, e.g. lobsters, they sometimes get the same name—"statoliths".

In twining stems the growing part shows a swinging movement, and also twists on its own axis. In this case the particular sensitiveness to gravity appears to be situated on one side or flank of the stem. More rapid growth follows the excitation, and as the swinging movement brings a new segment of the stem into the flank position, the twining continues.

But the directed obligatory movements or tropisms may be responses not to gravity, but to other stimuli. Thus tendrils respond to repeated contact, such as the slight rubbing of a twig, though not to the fall of a drop of quicksilver, or the touch of a perfectly smooth thread of gelatin. Or the stimulation may be moisture, or diffusing chemical substances, or light.

When there is a power of free locomotion, as in some simple Algæ, Fungi and reproductive cells, there may be an automatic adjustment of the direction of movement in reference to the direction of the localised stimulus. The movement may be towards or away from the provocation, which may be of various kinds, such as light or a chemical substance. It is probably in this way that motile male cells find the female cell which they fertilise.

When there is free locomotion it is convenient to use the terms chemotactic, phototactic, and so on; when the plant is fixed but moves a part in any plane, determined by the direction of the stimulus, it is usual to speak of tropisms; but a curvature confined to a single plane is spoken of as nastic, e.g. photonastic. In some cases, as in a tendril bending round its support, the stimulus acts as a trigger-pulling or releasing cause, for beyond a minimum limit, a slender twig is as effective as a much heavier one. In other cases, such as a growing plant in a room illumined through a single window, there is some correlation between the amount of the stimulus and the amount of the curvature towards the light. Yet it is not possible to explain the phenomena in any simple or direct way, e.g. by simply saying that growth is quicker on the relatively more shaded convex side, the rate of growth being retarded by light. For we have to

take account of the internal structure and activities of the parts concerned, and of such puzzles as the reversal of the phototropism in certain circumstances. Thus the flower-stalk which spreads the flowers of the toad-flax (*Linaria Cymbalaria*) to the sun, may at a later stage become negatively phototropic and push the fruit into a crevice in the wall.

Opening and Closing of Flowers.—While the growth-movements of a shoot bend it in turn to all points of the compass, the movements of leaves and floral parts are in one plane. The leaves rise and sink; the flowers, or it may be inflorescences, open and close. As long as there is some growth in the leaf or its stalk, in sepal, petal, or bract, these so-called "nastic" curvatures occur. The crocus flower opens in warmth and closes in cold; the dandelion inflorescence opens in sunshine and closes on a cloudy day. So definitely sensitive are some flowers to the external changes of illumination and temperature that attempts have been made to arrange a "floral clock" with a succession of plants opening at successive hours; but the clock has, of course, to be consulted good-humouredly. All the movements of this "nastic" type depend on the unequal growth of the two surfaces of the organ. Thus, under increased warmth the inner faces of the parts of the tulip perianth grow more rapidly than the outer faces, and so the flower opens.

Motor Organs.—In some cases there are special motor organs at strategic points, and these effect the movement of parts by rapid changes in the turgidity of some of their component cells. Thus at the bases of the leaflets in the clovers and wood-sorrels there are specialised cushions, which fold the leaflets together into a "sleeping" position, and raise them again when the conditions change. Similarly at the bases of the pinnules of the Sensitive Plant, at the base of the four divisions of the leaf, and at the base of the main leaf-stalk, there are motor "cushions". The stamens of the barberry, which move when touched by an insect-visitor's feet (or in experimental conditions by a bristle), have a basal motor organ. Another familiar instance is the bilobed stigma of the musk (Mimulus), which closes on pollen grains or when artificially touched with the tip of a leaf of grass.

In a typical motor organ at the base of a leaflet, there is a rind of thin-walled sappy cells, and the fibro-vascular bundles lie close together near the centre. When the turgor or hydrostatic pressure of the cells on one side or surface of the cushion is lessened, that side or surface becomes concave, and this brings about a movement of the distal part. A recovery from the flaccid state of the cells reverses the movement; and all the plant's movements brought about by changed permeability and turgor of cells are similarly reversible.

The stimuli which induce the turgor movements may be changes in illumination and temperature, as in the badly named "sleep"

movements of leaves at nightfall. Often, however, the stimulus is some contact, as in the Sensitive Plant and Venus's Fly-trap. On the other hand, there are similar movements (autonomic as distinguished from paratonic) for which it is not at present possible to suggest any particular stimulus. They are sometimes called spontaneous, and the most striking instance is that of the Indian Telegraph Plant (*Desmodium gyrans*). The tripartite leaf has a median leaflet, which is depressed and raised again in response to stimulation, and two minute basal leaflets, which exhibit spontaneous movements, somewhat semaphore-like, sometimes uniform, but usually jerky. They fall rather more rapidly than they rise, and a complete double movement takes 2–4 minutes. "As the turgor variations tend to fluctuate regularly to right and left of the vertical plane, the tip of each leaflet describes a narrow ellipse." The movements cease in adverse conditions, but their significance is unknown. It is probable that there are many similar autonomic movements which are on so small a scale that they remain unnoticed.

Summary.—Apart from the locomotion of entire plants, such as some simple Algæ, and of germ-cells, such as the male elements of ferns, we may distinguish among plants (*a*) the all-round growth-movements, such as nutation, (*b*) the movements in one direction, induced by differential growth, provoked by stimuli acting on a given internal structure and state of activity, e.g. heliotropic bending to or from the light; (*c*) turgor movements, usually localised in special organs, induced by differential permeability of cell walls, and provoked by stimuli, as in the Sensitive Plant; and (*d*) autonomic movements, apart from recognisable stimuli, as in the Telegraph Plant.

Are Plants Nervous?—As we have already emphasised, a great step towards unity of outlook was marked by Claude Bernard's *Leçons sur les Phénomènes de la Vie communs aux Animaux et aux Végétaux* (1879). It became clear that plants and animals share a common life, though their detailed expressions of it are very different. The beech-tree feeds and grows, digests and breathes as really as does the squirrel on its branches. In regard to none of the main functions except excretion is there any essential difference. Moreover, many simple plants swim about actively; growing shoots and roots have gently-swaying tips; leaves rise and fall, flowers open and close, with the waxing and waning light of day. The tendrils of climbers, the leaves of the Sensitive Plant, the tentacles of the sundew, the blade of Venus's Fly-trap, the stamens of the barberry, the stigma of the musk, and many other plant structures exhibit exquisite sensitiveness. In the sense of answering back to stimuli, they *feel*. How far we have got from the aphorism of Linnæus: *Lapides crescunt; vegetabilia crescunt et vivunt; animalia crescunt et vivunt et sentiunt*. The "nervousness" of

plants is now recognised by all, and for driving this conclusion home by persistent and ingenious experiments great credit is due to Sir Jagadis Chunder Bose. See, for instance, his *Nervous Mechanism in Plants* (1926).

When the glowing but not flaming tip of the long thin incense stick of the Chinese is applied to a secondary rib of the beautiful compound pinnate leaf of the Sensitive Plant, *Mimosa pudica*, the result is a spreading impulse, reminding one of the nervous impulse in an animal. The leaflets close together from below upwards; the secondary ribs or stalks draw together as in a folding fan; the leaf as a whole sinks down when the stimulus reaches the motor cushion

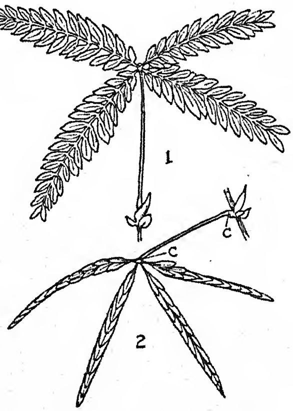


FIG. 46.

Leaf of the Sensitive Plant (*Mimosa pudica*). 1, fully expanded; 2, in pendent position, with pinnules folded upwards.

or pulvinus at the base of the main leaf-stalk; the impulse passes into the stem and other leaves collapse; if the stimulus be strong enough, the impulse, whatever it is, may ascend to the apex of the stem and travel down the other side. Of course, there is nothing but convenience in using an incense stick; a scratching pin will do as well provided that the stimulus is superficial. It must not injure the surface, nor cause exudation of sap, nor irritate the enclosed wood. The central problem is the *conduction* of the excitation from the place stimulated to a distance in the plant where a motor organ or pulvinus is activated. Is the conduction like that which passes along the nerve-fibres of animals?

Bose comes to the deliberate conclusion that the higher plants have a well-defined nervous system. Excitation from part to part is conducted by the phloem or bast of the fibro-vascular bundle. The excitation is not due to the movement of fluid in vessels or cells, as in the sap-currents; it is of the nature of a protoplasmic thrill, as in

an animal nerve. Moreover, the idea of a reflex arc is boldly extended from the animal to the plant. In the animal a stimulus excites the ending of a sensory nerve-fibre, the thrill passes to the sensory nerve-cell, thence to an associative or communicating nerve-cell, thence to a motor nerve-cell, and thence by a motor nerve-fibre to the muscles which contract. So, before we can say "reflex action", we draw our finger away from a hot object. But there is a similar phenomenon, according to Sir Jagadis, in the Sensitive Plant. If a very slight stimulus be applied to one of the secondary ribs of a leaf, it gives rise to an ingoing impulse causing the characteristic response in a part of the motor cushion or pulvinus; and that is all. But if there be a slight increase in the intensity of the stimulus, a new phenomenon makes its appearance; the ingoing or afferent impulse, reaching the centre (perhaps a question-begging term), becomes reflected along a new path as an efferent impulse. If these conclusions are established up to the hilt, the work of Sir Jagadis is of the highest importance, for it means not merely that phenomena analogous to animal reflex actions occur in plants, as has been often suggested, it means that plants may have nervous reflex arcs precisely comparable to those of animals.

Whatever conclusion be reached on this crucial question we cannot but admire the ingenuity of the experimenter's methods. Thus by a refinement of the electrical stimulation he secures a controlled amount of stimulus. Thus, again, he has improved the methods of recording both the leaf movement and the electrical responses, so reaching a more exact timing of the rates of conduction and reaction. Science, it has been said, *begins* with measurement; the advance Sir Jagadis has made shows how it is *continued* by measurement.

Among the new facts brought forward in this continuation of his always suggestive and brilliant researches, three may be noted: (1) The motor cushion at the base of the leaf-stalk has four different quadrants which bring about different movements—up and down, left and right. More than that, there is a definite nerve-connection between each of the four leaflets and a corresponding quadrant of the motor cushion. This is very striking, not to say strange.

(2) The movement of the leaf of the Sensitive Plant is brought about by changes in turgor (or intracellular pressure) in the motor cushion or pulvinus. When a stimulus is applied directly to the cushion, the leaf falls in about 0·1 of a second. If the stimulus be indirect, i.e. at some distance from the pulvinus, there is a longer interval before collapse, and during this interval there is a weak upward movement, which Sir Jagadis calls erectile. Generalising from this, too quickly perhaps, he defines the effect of direct stimulation as a diminution of turgor, consequent contraction, diminished rate of growth, and the negative response—the *sinking*

down of the leaf. Distinguished from this is the effect of indirect stimulation of feeble intensity, for it implies increase of turgor, expansion, accelerated rate of growth, and the positive response—the *erection* of the leaf. Here, we confess, the alert experimenter moves too quickly for us.

(3) Very striking—we wonder how it had been missed—is the observed fact that an excitation may pass up one side of the stem and down the other.

These are three of the many new facts expounded in Bose's fascinating volume, the main result of which is the certainty that the plant is a more "nervous" organism than has been supposed. But behind the facts is the interpretation. The conduction of the excitation is probably by elongated cells of the phloem and the bundle-sheath as it is called, but the analysis of the path does not prove that these elements are in the strict sense nervous. We cannot go further than say that in our judgment Bose works out a very suggestive parallel between the conducting system in plants and the nervous system in animals. But we do not think that he allows enough for the alternative interpretation in terms of the diffusion of fluids and of the hormones which they may contain. The work of Ricca and of Snow demands fuller consideration. But even if Sir Jagadis's interpretation fails to convince, his facts are illuminating. He corrects Linnæus: *Vegetabilia sentiunt.*

THE ORGANISM AS MECHANISM, YET MORE.—It is an old story, as biology goes, that the green plant seizes and applies the energy of light to its nutritional and constructive advantage, and is thereby physiologically distinguished from ordinary animals, and from such non-chlorophyllian plants as moulds and mushrooms. Bergson however (in *Creative Evolution,* Chap. II) has made fuller use of this familiar conception for his criticism of the strictly mechanistic view of physiological processes; and Prof. Johnstone, in his valuable *Philosophy of Biology* (1914) and in *The Mechanism of Life* (1921), has developed this criticism with vigour and fullness. The general processes in non-living or physical Nature and of man's machines agree in running down, and that irreversibly, towards that degradation of energy which Kelvin called its dissipation, but which is better described as from minimum to maximum entropy—that inertness of universally uniform temperature, the "warm-death" (Wärmetod) of Clausius, in which all physical processes seem as yet destined to end, so far as the doctrine of energy yet goes.

But the processes of life—and these not only in the green leaf, but in various measure throughout all constructive metabolism, of animal and plant alike—exhibit a reversal of this process; so we have here a diagnostic character between living beings and the inorganic world.

The past century's synthetic achievements of the organic chemists, as from Wöhler's production of urea in 1828 to Fischer's sugars and more in current progress, have long appeared to support the mechanistic philosophy of life. But here Bergson and Johnstone reply that such marvels are after all but fresh examples of man's best functioning as regards Nature; in which—despite an industrial age characterised by the so-called "development" of natural regions, but too largely a dissipation of their energies—he is now beginning to return to his normal human and even organic task, that of the reaction of life against the physical running down of the Universe towards maximum entropy.

That such a termination for the entire Universe is not entirely to be feared, is argued from the fact that as the astronomer (on the large scale, if not this solar and planetary one) can conceive of no beginning, but only of the past as practically (if not speculatively) eternal, this conclusion of its activities should already have arrived, were there not also in the Universe a compensatory process—somewhere and somehow—though as yet he knows not where, nor how. It is thus something encouraging and suggestive towards future inquiry, that—albeit within the small planetary experience to which we are in this respect so strictly limited—we should find in the processes by which organic life sustains itself (and even in the experimental syntheses in detail which we are learning to accomplish), some clear evidence that the reversibility of the general dissipation and degradation of energy is conceivable; since here, on our small world, we see it on a scale sufficient to sustain the activities of life; indeed, even characterising them.

THE CIRCULATION OF NITROGEN.—Living matter always contains a mixture of proteins, which are complex nitrogenous carbon compounds. It follows that there must be nitrogen in the food. Animals get their nitrogen supplies by eating other animals or from vegetable food. Plants get their nitrogen supplies from nitrates and the like in soil. The nitrates and other nitrogenous compounds in the soil are due to the action of nitrifying bacteria which work on the ammonia that results from the decomposition of decaying organic matter or from the waste-products of animals. The bacteria in question oxidise the ammonia into nitrous and nitric acids which plants can utilise. There are other denitrifying bacteria, however, that break up nitric and nitrous acids and return the nitrogen to the immense stock that there is in the atmosphere. This atmospheric nitrogen may be captured and fixed in natural conditions by electric discharges, as in thunderstorms, or by the quiet and rather mysterious work of certain bacteria that live in partnership with various kinds of plants, especially those of the pea and clover order (Leguminosæ). So a nitrogen-circle may be like this: Atmospheric

nitrogen is captured by help of symbiotic bacteria; nitrogenous compounds are formed in the living Leguminous plant; the decaying plant is worked on by other bacteria, and ammonia results. The ammonia is oxidised into nitrous and nitric acids by help of other bacteria; and thus is formed the nitrogenous food of plants. Or another circle may begin with seeds rich in nitrogenous compounds which are eaten by animals, which give off nitrogenous waste; and this, breaking down into ammonia, is oxidised by bacteria into forms that plants can use. But in various ways there is apt to be considerable loss of available nitrogen. This happens when a forest is burnt or a shot is fired, for freed nitrogen joins the supply in the air. There is wastage also when sewage passes into the sea, since the ammonia or the like cannot be captured again except by seaweeds, which man has not yet learned to use to much purpose. There is also a locking up of nitrogen compounds in inedible plants, especially if they cannot be ploughed into the soil. Thus the soil tends to be impoverished as regards its nitrogen compounds; so manuring is necessary, whether with the refuse of the farmyard or with nitre from the beds formed long ago in Chile and Peru. This lends great interest to the work of the symbiotic bacteria, which are able to capture (we do not yet understand *how*), some of the free atmospheric nitrogen, which is also present in ordinarily aërated soils. Just as interesting are man's devices for fixing the nitrogen of the air by forcing it to unite with oxygen, the coercion being provided by a powerful electric arc, which again may be the transformed power of a waterfall. Nitrogen may also be coerced into union with hydrogen, with carbon, with silicon. In other words, the synthesis of ammonia, cyanides, and nitrites has been effected, and the atmospheric reservoir has been tapped.

CHEMISTRY IN THE SERVICE OF BIOLOGY

Biology occupies a central position among the sciences, with psychology and sociology above it, with physics and chemistry below. It is impossible that psychology and sociology should dispense with biology, for man is an organism—feeding, working, developing, growing, struggling, evolving, and these are problems of biology. Moreover, the study of mind cannot be safely separated from the study of body: *nemo psychologus, nisi physiologus*—that is to say, the psychologist must also be a physiologist. But let us not forget the vice versa!

In the same way it is impossible that biology should dispense with the assistance of physics and chemistry, for the organism is a material system adjusted for the transformation of energy, and whatever else living may mean, it implies a routine of chemical reactions.

There is a physics and a chemistry of the living body, and though they do not when added up fulfil the rôle of biology, they are indispensable aids to our understanding of the living creature.

Our inquiry, then, is this. What big contributions has chemistry made to biology, and what is it doing for biology to-day? It is plain that *most* of the contributions must be to the physiological side of biology; yet we shall see that chemistry is also helping embryology, ecology or natural history, and even evolution theory. There is necessarily some overlapping in this discussion; yet it is worth while, for our object here is what might be called methodological, to illustrate from various sets of facts the indispensability of chemistry to biology.

There is no doubt as to where we should begin, for the initiator of modern biochemistry was Lavoisier, at the time of the French Revolution, that ill-fated genius whom the "Reds" of the Terror guillotined, their very judge crying out in his madness that "the Republic has no need of savants". Utilising the clue afforded by Priestley's discovery (or re-discovery) of oxygen, Lavoisier first made it clear that living implies combustion or oxidation of carbon compounds, with the liberation of an oxide of carbon as a waste-product. Lavoisier showed that life was literally a flame; he put the living creature beside the lighted candle, and henceforth the burning bush became the symbol of the living organism.

Another of the fundamental contributions was made about half a century later by the famous Liebig. For our present inquiry there is great significance in the title of his well-known book (1840), *Chemistry in its Applications to Agriculture and Physiology*; but we wish mainly to associate his name with an idea that is fundamental in physiology—the Circulation of Matter. Everyone is now familiar with the flux of molecules from one linkage to another, the ceaseless dance with changing partners, the passage of material from one embodiment to another. Whether we think of the nitrogen cycle, the carbon cycle, the sulphur cycle, the iron cycle, or any other, we come in touch with biological problems of nutrition, development, growth, and more besides. Animate Nature has evolved on a plan that necessitates a cycle of reincarnations. All flesh is grass and all fish is diatom; and so the world goes round. Recent pioneering work at the Rowett Institute at Aberdeen, on the importance of the mineral constituents in the food of mammals and birds, illustrates the far-reaching influence of Liebig's great idea.

In some cases chemistry made contributions whose import was hardly realised at the time, yet has continued increasingly. Thus, about a generation after Lavoisier, a great step was made in Wöhler's synthesis of urea (1828). This was an epoch-making event, for the building-up of this organic substance from simple inorganic materials broke down at one blow the blockading wall between what

goes on in non-living Nature and what goes on in the living body. It was at a stroke the death-blow to the doctrine that organic substances could not be made except by organisms; and it was the beginning of that brilliant succession of synthetic achievements which have yielded not only sugars and alcohols, but such complex compounds as salicylic acid, indigo, madder, amino-acids, adrenalin, and thyroxin. The synthetic chemist is drawing near to the artificial production of proteins—hammering at the gates of Life's citadel. But apart from the synthetic triumphs which followed, and still follow, Wöhler's unsensational step, there was the blazing of a new trail. The products and processes of the living body were no longer a preserve for the physiologist, they were recognised as amenable to chemical analysis. It was on a stage beyond Lavoisier's the beginning of biochemistry.

Another great initiator was Pasteur, chemist more than biologist, who advanced logically from his study of tartrates, not only to a recognition of the manifold activities of bacteria, but to some pre-vision of the part that ferments or enzymes play in vital processes. It is a commonplace now that we cannot understand either the rapidity or the relative tirelessness of metabolism unless we take account of the ceaseless fermentations.

But while we cannot but look upon Pasteur as a great initiator, profoundly influencing biology, we would not dwell on this, since the study of ferments began with an investigation of fermenting organisms, like the yeast-plant, and the transference of attention to non-living enzymes came later. It might fairly be said, we think, that in connection with ferments biology was at first in the service of chemistry, rather than the other way round. Moreover, bacteriology is an inseparable field of biology.

Our treatment must be simply illustrative; and as instances of the indispensability of chemistry to biology we would select (*a*) the study of the photosynthesis that goes on in every sunlit green leaf, and (*b*) the study of the properties of matter in a colloidal state. The late Sir William Bayliss spoke of the action of chlorophyll as "perhaps the most interesting of all natural phenomena"; and he might have added what he meant, that the photosynthesis brought about in the green leaf is the most important process in the living world. It produces the food on which all animals and mankind ultimately depend; and it has made and continues to make the oxygen we breathe. Now the study of the fundamental work of the green leaf began among the chemists, and it is still continuing among the chemists. Recall the early steps, how Priestley showed (1774) that air "spoilt" by mice is made good again by sprigs of green mint; how Ingenhousz showed (1780) that the sunlight is necessary for the liberation of "dephlogisticated air", afterwards called oxygen; and how Senebier showed (1783) that what occurs is

the conversion of "fixed air" or carbon dioxide into "dephlogisticated air" or oxygen. Let our thoughts run on for a century and a half or so; and we now read that chlorophyll is a complex of four pigments; that the most useful rays are the reddish rays; that the light is probably transformed to electricity, which reduces the carbonic acid to formic acid (CH_2O_2) and later to formaldehyde (CH_2O), a molecule of oxygen being set free as a by-product—a precious by-product by which we live. Then comes the main product, glucose, and the end-products are proteins. Without chemistry it is all "joukery-pawkery". But let our thoughts go once more to Prof. Baly's laboratory, in Liverpool, where the students can sweeten their tea with synthetic sugar built up by the light of a mercury vapour lamp shining through a vessel containing carbon-dioxide and water. Thus the work of the green leaf is mimicked in the test-tube by the production of formaldehyde, and later on of sugar, from carbon dioxide and water. Let our thoughts go on still farther, to the very interesting chemical analogy between chlorophyll and hæmoglobin; but this takes us into deep waters!

Chemistry and physics have joined hands so firmly in recent years, that demarcation of the fields of inquiry is practically impossible; and therefore we need not apologise for taking as our next illustration the study of colloids. It is not too much to say that our view of the activities that go on in the living cell has been almost entirely changed by a knowledge of the properties of matter in a colloid state; and we may date the beginning of this knowledge from Thomas Graham (1861). Living matter is in a colloidal state; that is to say, there are countless ultra-microscopic particles and droplets suspended or dispersed in a more or less liquid medium. The boundary surfaces of contact between the countless particles or droplets and the medium are enormous in proportion to the total mass, and on these surfaces there is room for a multitude of chemical and physical actions to take place. This fundamental fact helps us greatly towards an understanding of the prodigious effectiveness of the living cell.

We have given two instances of foundation-stones (laid by Lavoisier and Liebig), two instances of the great initiatives (on the part of Wöhler and Pasteur), two examples of fundamental contributions still being added to (the study of photosynthesis and colloids); and now we must be content to take two examples of distinctively modern contributions. We would refer first to the discovery of glutathione by Gowland Hopkins in 1921. This glutathione is an organic substance, falling naturally into three parts, all of which are amino-acids—glycine, glutamic acid and cystein—and it will, of course, be kept in mind that the most essential components of living matter, the proteins, are chains of amino-acids. The most important property of glutathione is that under

certain conditions, realised in the living cell, it reacts with the oxygen externally supplied, and is able to pass it on indirectly to the food-materials in the tissues. It was a great step when Lavoisier put the living organism beside the lighted candle and elucidated the combustion or oxidation going on in both; but there has always been the lurking difficulty that the numerous and very rapid energy-yielding reactions in the tissues take place at a low temperature. This is now explained by the discovery of the "oxygen-transporting" function of glutathione, which is widely distributed in plants and animals. Here one might continue the subject by referring to Keilin's discovery of a widely distributed cell-pigment, cytochrome, which has to do with the control of oxygen within the cell.

As a second modern example of the assistance that chemistry is always giving to biology, we may take the contraction of muscle, the subject of more investigations than any other function. The problem of the contraction of a muscle fibre is still but partially solved, but our point at present is simply this, that its aspect was entirely changed by the chemical researches of Fletcher and Hopkins. These researches showed that the stimulation of the muscle fibre is associated with the liberation of lactic acid, which in some way or other induces a physical change in the muscle fibrils, namely, contraction. It may be, as we have seen, that the liberated lactic acid raises the surface-tension at the surfaces at which it is produced, so that they tend, for instance, to become more spherical, or it may be that the production of lactic acid within a semi-permeable membrane attracts water and induces swelling. This does not concern us just now: the point is that a chemical change, in which there is production of lactic (and perhaps phosphoric) acid, induces a physical change; and that the production of lactic acid is essential. Thus we can understand better why there must be a reinstatement of the lactic acid or its chemical precursor into the fibre if it is to continue effective; and there are interesting theories which suggest *how* this restitution of lactic acid may be effected. But the point is that, even with the everyday function of contractility, progress in understanding is largely dependent on chemistry and physics.

Now, we might continue with other functions of the body, and show how chemistry helps the biologist to understand them; but our study cannot be more than illustrative. Moreover, it must be noted that in many cases, like the circulation of the blood, physics has more to say than chemistry. As to endocrinal influences and reflex actions, neither chemistry nor physics has as yet any illuminating suggestion to offer. So we change our outlook.

Sometimes it seems fair to say that the help chemistry gives biology is not so much an idea as an opportunity. When Lavoisier said "living is burning", that was a clarifying idea; but it is other-

wise with the modern experiments on inducing artificial parthenogenesis by means of chemical reagents. For the chemical provocatives are so diverse that they do not in themselves throw any light on what results—the launching of an unfertilised egg on the voyage of development. When Delage added tannin and ammonia to the sea-water in which unfertilised sea-urchin eggs were floating, they began to segment and develop, and when they were restored to normal sea-water the development went on apace and quite normally, so that fatherless sea-urchins were reared. But Loeb did the same by subjecting the eggs of sea-urchins for a very short time to the influence of butyric acid, and then restoring them to normal sea-water. There are other ways in which artificial parthenogenesis can be brought about, but they do not yet throw much light on the normal process of fertilisation. One can say this much, however, that what the living sperm effects, as far as stimulus goes, may be effected by chemical reagents.

It is not always easy to draw a line between help with a chemical method and help with a chemical idea; and an illustration of this may be useful. A Russian physiologist, Dr. E. O. Manoilov, claims to have discovered a reaction by which it is possible to distinguish the blood of a female from the blood of a male. To the blood in a test-tube one adds in succession some papayotin, some methyl-green, some potassium permanganate, some hydrochloric acid, and some thiosinamin (it is unnecessary to mention the strengths and quantities). The outcome is that the blood of the male soon becomes colourless or nearly so, while the blood of the female retains its reddish colour. This has been verified for mice, sheep, pigeons, and so on. The same is said to be true in regard to plants, with separate sexes so-called, like the nettle, the diœcious Lychnis, the dog's mercury, the willow, and the poplar. It has been successfully tried for both animals and plants at the Cold Spring Harbour Experimental Station in America; but tests made by one of the demonstrators in the Aberdeen University Zoological Laboratory were quite inconclusive. Some gave the right result, some the wrong, and some nothing. That is by the way; for the point is this, that if the chemical treatment, or another like it, does actually serve to differentiate the blood of a male from the blood of a female, or the extract of a male plant from the extract of a female plant, it should be possible to discover the chemical reason—a discovery which would afford a clue to the lasting puzzle as to the essential metabolic difference between maleness and femaleness.

A simpler test has been used by Steele and Zeimst. Hydrochloric acid and an oxidising solution are added to a diluted sample of blood serum in a test-tube. A few drops of methyl-green are added, and if the blood is from a female the colour is green, if from a male the colour is red. Twenty pigeons and seventeen cattle were tried

with correct results; sixty-three fowls were correctly diagnosed out of seventy-seven.

Sometimes the aid that chemistry gives is of the nature of a technical method; thus the elegant Japanese instrument called a biometer, which measures very minute quantities of carbon dioxide, is used in estimating the intensity of metabolism at different parts of an animal, and has helped towards the establishment of the profoundly important biological idea of metabolic gradients of intensity. Thus we know that in a simple worm the intensity of the vital processes wanes from the head and backwards for a certain distance. Here we should take cognisance of the marvellously exact methods of micro-analysis devised by Prof. Pregl of Graz, a Nobel prizeman, who has made it possible to deal with very minute quantities of significant organic substances, such as the pigments of a butterfly's wing.

In studying the minute structure of cells it is often useful to have differential stains, such as the so-called "basic" stains, which colour more especially the nucleus, and the so-called "acid" stains, which have more affinity for the cytoplasm. It is now believed that the process is rather physical than chemical, the "basic" dyes being precipitated on the surface of the more solid constituents of the cell, while the "acid" dyes act by soaking or "seeping" in at various speeds. Till recently, however, differential staining was interpreted chemically, and it may be recalled that the possibility of differentially dyeing bacteria in a preparation led Ehrlich to the search for a dye which would kill microbes without doing harm to the tissues. In fact, a probably mistaken interpretation led to such valuable drugs as salvarsan and "Bayer 205".

It must not be supposed that chemistry helps only in regard to physiology. A suggestive instance of the light that chemistry may throw on the problems of development is Dr. E. I. Werber's experiment with the developing eggs of the American minnow (Fundulus), which he subjected to various reagents, especially butyric acid, with the result that he provoked many different kinds of monstrosities —in eyes and ears, nostrils and mouth, fins and heart. The butyric acid seems to disarrange, and partly dissolve, the essential germinal material, especially towards the head end; hence monstrosities. Now, it is interesting to note that when the metabolism of carbohydrates goes wrong in a mammal's body, one of the results of the disturbance may be derivatives of butyric acid. But if a mammalian mother's constitution were thus poisoned by the production of butyric acid, this might be the cause of monstrosities in the embryo; a fresh light on a very old problem, and a light coming along what might be called a chemical avenue.

How can chemistry help with natural history or ecology, the study of organisms in their natural relation to surroundings, both animate

and inanimate? An illustration will answer. The physiologist is interested in pigments like hæmoglobin and chlorophyll, for their utility to the organism is fundamental. But there are many other pigments that have not this directly useful rôle, though they are secondarily of great value in concealing the animal, or advertising it, or dressing it in bright attire useful in courtship. These secondary utilities are often demonstrable, and it is reasonable to suppose that the coloration might be gradually elaborated by Natural Selection. Yet the difficulty has been to explain how the coloured material is there at all; and it is here that the biochemist comes in, by telling us the chemical nature and the probable derivation of the pigments in question. Thus he tells us that the green biliverdin of the Vertebrate's bile and of some tissues in Invertebrates may be regarded as a degradation product of hæmoglobin. Similarly, the dark melanin pigments of dark hair, feathers, skin, and so forth, are derivable from some of the abundant amino-acids (like tyrosine) into which proteins break up. The ruddy lipochromes—so widely distributed, as from the Norway lobster to the wattle of the red grouse—are traceable back to leaf pigments, which may be taken into the animal directly or indirectly as part of the food. The point should be clear. Given a natural supply of certain pigments which can readily be accounted for in the chemical routine of the body, we are in a better position to understand their secondary utilisation. They are there for the using, so to speak—for the using if needs be—in the everyday life of the creature, whether as protection, or warning, or decoration.

Can chemistry also be of service in the working out of a theory of organic evolution? The question is almost answered in the asking; for organisms evolve in a chemical and physical environment with which they are in intimate and subtle relations. A slight difference in the nutrition and environment of two apparently identical larvæ (of the green worm Bonellia), and one becomes a large independent female, the other a pigmy parasitic male. That is for the individual, but the same kind of influence must also have affected the race. Hereditary nature and environing and functional nurture work into one another's hands; both are components of the resultant—developmental and evolutionary alike.

But if we consider such a fine piece of work as Gautier's analysis of the serial chemical differences between different varieties of grapes, or the memoir of Reichert and Brown on the differences in the hæmoglobin of even nearly related mammals, we get a glimpse of another important and promiseful contribution, for there is a chemical basis for species. All flesh is not the same flesh; but there is one flesh of man and another of fishes. Every type has its own protein; there is a chemical accompaniment of individuality.

What will be left when the chemistry and the physics of the living body have continued their work for several centuries? A

clearer, firmer biology. For the biologist has questions of his own to ask and answer, which are beyond the scope of chemistry and physics as we know them to-day. For him the living organism is an individuality—not a vat or an engine. It is an integrate, suffused with awareness and with some measure of endeavour. In many cases it has clearly a mind of its own. In its reproduction, development, and purposive agency, in its heredity, variation and evolution, the organism transcends chemistry and physics. There are treasures in its sea which cannot be caught in the meshes of the chemical and physical net. The organism is alive.

THE CHEMISTRY OF THE ANIMAL BODY

1. THE FOOD AS A SOURCE OF ENERGY.—In the chapter of this book which deals with the living cell, it is explained that the energy of the animal body has its source in the chemical reactions which go on there, and that by far the most important of these reactions are *oxidations*. In typical cases, the carbon of the food is oxidised to carbon dioxide, and the hydrogen to water. It will be explained later that the animal has certain particular chemical requirements, but as far as energy-output is concerned the essentials are that there should be a sufficient supply of organic food-material (containing carbon and hydrogen), and sufficient oxygen to combine with it. These, it may be recalled, are also the chemical requirements of the internal-combustion engine.

Just before the French Revolution, Lavoisier had shown that a candle was able to give out energy—light and heat—because it oxidised carbon to carbon dioxide; he went farther and, aided by the great physicist Laplace, showed that the same thing was true of the animal body. His apparatus was rough and ready, and he failed to avoid several pitfalls; but he successfully proved his main points. He could find out how much carbon an animal burnt in a given time, by measuring the amount of carbon dioxide which it breathed out; and at the same time he measured the amount of heat produced by the animal, and compared these figures with the amount of heat generated by an equivalent amount of carbon burnt in a laboratory experiment. He found that nearly the whole of the heat of the animal's body was due to the combustion of carbon. He also knew that some of the oxygen used up combined with hydrogen, but it was not till somewhat later that Dulong and Depretz were able to draw up satisfactory balance-sheets in which the amounts of oxygen used up, of carbon dioxide and water produced, and of energy evolved, corresponded reasonably well. In the meanwhile, however, Lavoisier had found that the body uses up far more oxygen when it is performing any sort of extra work—muscular

work, or even digestion—than when it is merely maintaining a constant temperature and performing the necessary work of breathing, pumping the blood through the arteries, and so forth. When the work of these French pioneers was followed nearly a century later by the precise studies of Rubner and others, real proof was obtained of what was even in these early experiments clearly indicated, that in its chemical exchanges the animal body is a machine, neither creating nor destroying energy, and obeying the laws of thermodynamics.

The three great classes of foods are carbohydrates, fats, and proteins; and the latter are of special importance, inasmuch as they serve to repair broken-down tissue and make good the inevitable wastage, as well as for new growth. Also requisite for the maintenance of life are certain inorganic salts, compounds of the rarer necessary elements, besides vitamins and other accessories, which are important by virtue of their chemical peculiarities, rather than because they act as chemical sources of energy. The proteins not only supply material for repair and for growth, they also serve to furnish energy to the body by oxidations, just as the fats and carbohydrates do. Not one of the three types of food is capable of yielding quite as much energy as an equal weight of pure carbon or hydrogen oxidised experimentally, for the reason that in these compounds there is already a certain amount of oxygen. Consider, for example, the case of the most typical and most important carbohydrate, glucose, whose chemical formula is $C_6H_{12}O_6$. As there is already enough oxygen to combine with all the hydrogen present to form water, it follows that no energy can be derived from the oxidation of hydrogen in the case of sugars. On the other hand, each of the six carbon atoms will combine with two atoms (one molecule) of oxygen to form one molecule of carbon dioxide, and this reaction will yield energy. For every molecule of oxygen used up when glucose or any other carbohydrate is burnt in the body, one molecule of carbon dioxide is produced; and since equal volumes of all gases under like conditions contain equal numbers of molecules, the ratio of carbon dioxide breathed out to oxygen consumed will be 1 : 1, by volume, when carbohydrates alone are being oxidised.

This ratio, the *Respiratory Quotient,* is of great importance as an index of the processes going on within the body. For if fats or proteins are being oxidised, the respiratory quotient will fall, perhaps to 7 : 10; the reason being that these substances contain proportionately less oxygen than carbohydrates, so that more oxygen must be breathed in if all the hydrogen atoms of the food-material are to be oxidised to water. In fact, while the carbohydrates, with such formulæ as $C_6H_{12}O_6$ and $C_{12}H_{22}O_{11}$, may be regarded as carbon *plus* water, the fats have the composition $C_{57}H_{110}O_6$, or something of the sort, that is to say, carbon *plus* water, *plus a large*

amount of oxidisable hydrogen. The same is true of proteins. A very interesting case is the respiratory quotient of hibernating mammals (marmots): within the body there takes place, it would seem, a conversion of compounds poor in oxygen (fats) into oxygen-rich compounds (carbohydrates), so that a large amount of oxygen is breathed in without the immediate appearance of a corresponding amount of carbon dioxide. The oxygen is, in fact, stored in the form of carbohydrate; for this reason the respiratory quotient falls extremely low, to about 3 : 10, in hibernating mammals.

A few approximate figures may now be given. Energy is required by the body for three chief purposes, to maintain constant temperature (animal heat), to vaporise water, and to do work—whether external as in moving, or internal as in the beating of the heart. It is not possible to reduce this output of energy, even at rest, below about 2,500 calories per day for an adult man; this is about the energy yielded by two pounds (one kilogram) of bread and meat. In addition, about 100 grams (quarter of a pound) of protein must be allowed for daily to make good the constant breakdown of the materials of the tissues themselves.

2. THE CHEMICAL ASPECT OF NUTRITION.—The preceding sentence leads naturally on to a consideration of the *chemical* requirements of the body, as distinct from its *energy* requirements. The distinction between these two aspects of the question of nutrition is made clearer if the case of the higher plants is considered. These are able, with the help of their green pigment (chlorophyll), to utilise the energy of the sunlight, with which they build up from carbon dioxide and water such compounds as starch and sugars, in which the energy of the sunlight may be said to be stored. But in spite of this independence of a supply of energy-containing food-materials, the plant has certain very definite chemical requirements—it must be supplied with nitrogen-containing compounds and with various inorganic salts. It is evident in the first place that plant and animal alike must be supplied with the chemical elements which enter into the composition of their tissues, since there is a certain amount of inevitable waste, and it is impossible to transmute one element into another. Apart from carbon, hydrogen, nitrogen, and oxygen, many other elements are essential to the life of the body, the most important being iron, sodium, potassium, and calcium among the metals, and sulphur, phosphorus, chlorine and iodine among the non-metals. All these, and probably several others, must be represented to some extent in a comprehensive diet. In some organisms, both plants and animals, there is a constant presence of rarer elements, such as arsenic, fluorine, zircon—a matter that requires further investigation.

The second feature of the chemical requirements of the body is related to the (limited) power of synthesis which the animal body

possesses, and to its likewise limited power of deriving energy from chemical compounds. The last point may be considered first. There are many simple organic compounds, containing oxidisable carbon and hydrogen, which nevertheless cannot act as sources of energy, for the mammal at least. Methane or marsh gas, CH_4, may be taken as an example; it could easily be used to furnish energy in an internal-combustion engine, and certain bacteria are able to live upon it; but the animal body is unable to oxidise it or to convert it into any oxidisable substance or energy-yielding compound. The supply of such compounds is dependent in the long run on the power of the green plants to form them by synthesis from simpler substances of lower energy content. In the same way, the nitrogen compounds required to form new tissue materials must be supplied in a sufficiently complex form; there are bacteria which can "fix" nitrogen gas from the air in the soil and soil-water, while the higher plants absorb nitrogen chiefly in the form of nitrates from the soil; animals, however, require still more complex nitrogen-compounds, for growth, at least, if not for maintenance, in the form of amino-acids (of which the simplest is glycine, $C_2H_5NO_2$) which they *are* able to bind together to form proteins. Animal and plant proteins break up to form simple nitrogenous compounds, such as urea (CH_4N_2O), which in turn are converted by soil bacteria to ammonia (NH_3). Other bacteria oxidise the ammonia, first to nitrites (as in the case of Nitrosomonas) and then to nitrates (as in the case of Nitrobacter). From these nitrates, such as saltpetre, the plants, starting the "nitrogen cycle" afresh, are able to form proteins.

Not only are animals unable to form amino-acids to any great extent, they are also unable, except in a limited way, to transform one amino-acid into another. As the proteins of the animal body are made up of many different amino-acids—glycine, alanine, leucine, cystine, tyrosine, proline, histidine, tryptophane, and so forth—it follows that nearly all or all of these compounds must be supplied in the food, either free or combined together as proteins, which can be split down in the process of digestion and built up again by the tissues. The protein of maize, for example (zein), is remarkable in that it contains no tryptophane, an amino-acid of great importance to the animal. Hopkins and others have shown that zein alone does not suffice as the protein element of the diet (of mice, in this particular experiment), but becomes adequate if tryptophane be added. From similar experiments has arisen the conception of the "biological value of proteins"—that some are more efficient foods than others because they cope more adequately with the special needs of the body.

There remains to be added to this account of the chemical requirements of the body one very important point already referred to. There are certain substances, the so-called "vitamins" or

accessory food-factors, of unknown chemical composition, of which small amounts must be present in the food if health is to be preserved, and especially if growth is to take place. These substances are known chiefly in a curious negative way, by the disorders which appear in the body if they are excluded from the diet.

For clearness we may sum up the various vitamins in tabular form—

VITAMIN A: in animal fats, green vegetables, etc.; promoting normal growth.

VITAMIN B: in outer parts of cereals and in yeast: anti-neuritic, preventing Beri-beri and some nervous disorders.

VITAMIN C: in oranges, lemons, sprouting peas, etc.; anti-scorbutic, preventing scurvy.

VITAMIN D: allied to A, fat-soluble, in animal fats like cod-liver oil and in green plants; anti-rachitic, promoting the absorption and utilisation of calcium and phosphorus, preventing rickets.

VITAMIN E: from the wheat-oil of sprouting grain, from lettuce, etc.; promoting successful reproduction in female rats; less securely known than the others.

There must remain some unsatisfactoriness in regard to vitamins until they are convincingly isolated and analysed. Some critics maintain that they are not special chemical entities, but rather physical attributes of certain constituents of the food. In this connection it should be noted that food which induces certain deficiency diseases in rats, may become satisfactory if irradiated with ultra-violet rays—a fact which may tell against the usual view that vitamins are specific chemical substances. The question often asked, How our ancestors flourished in ignorance of vitamins, must be answered in two ways: first, that they did not always flourish, as the terrible tales of scurvy show; and, second, that most mixed meals of unsophisticated food include an abundant supply of vitamins.

3. DIGESTION AND ABSORPTION.—The process of digestion is a process of simplification of the complex organic compounds of the food, and this simplification has two aspects. In the first place, when a protein from the food is to be used as a source of protein for the body, it is evident that it must first be reduced to their "highest common factor", to use an arithmetical analogy; and this highest common factor is naturally a mixture of the amino-acids of which all proteins are composed. In the second place, proteins, fats and complex carbohydrates cannot pass into the cells lining the intestine and so into the body, unless they are first greatly simplified in structure; the cells appear to be impermeable to the larger molecules.

This process of simplification which goes on in the alimentary canal is carried out by the action of the digestive juices secreted into the canal by the gland-cells which line it at many points or by associated glands; and the most important constituents of these juices are the enzymes. Enzymes (which are discussed in the chapter on the Cell) are colloidal organic substances of unknown nature which *catalyse*—that is to say, *hasten by their presence*—reactions which otherwise would proceed too slowly to be effective. The saliva, for example, though primarily a lubricating fluid, contains an enzyme (ptyalin) which splits up the large molecule of boiled starch.

The digestive juices of the stomach contain a large amount of hydrochloric acid, which is secreted by certain cells of the mucous lining. This acid greatly aids the action of the enzymes, as well as being of itself a powerful antiseptic. There are probably two distinct enzymes of importance in the stomach; one of which (rennin) attacks the protein of milk, causing clotting, while the other (pepsin) commences the long work of splitting up proteins in general, by forming simpler and more soluble compounds (metaproteins and proteoses).

From the stomach the partially digested food passes into the duodenum, where yet other digestive juices begin to work. The walls of the duodenum itself secrete a fluid which has only a weak digestive action, but which is strongly alkaline in reaction and aids the powerfully digestive pancreatic juice. Various substances may also be cast out of the body by way of the duodenal secretion, especially if the kidneys are not working well, but these are always liable to be reabsorbed by the intestine.

Closely applied to the outside of the duodenum is a compact gland, the pancreas, whose secretion enters the gut by two or more ducts. This secretion is also alkaline, so that the hydrochloric acid from the stomach is more than neutralised. There are also present several important enzymes; one of these (steapsin) attacks fats, splitting them into glycerol and fatty acids, and another attacks starch (amylopsin), forming from it the sugar maltose. Very important also is the substance *trypsinogen*, which is itself inactive, but which is speedily converted by an enzyme (enterokinase) into the enzyme *trypsin*, which digests the proteins already simplified by the pepsin of the stomach. Unlike pepsin, trypsin acts best in alkaline medium, such as is found in the gut at and below this point. There are present also, here as in the secretion of the duodenum itself, enzymes which convert the more complex sugars (maltose, lactose, cane sugar, with twelve carbon atoms) into simpler ones (glucose, $C_6H_{12}O_6$).

Close to the point where one of the pancreatic ducts enters the duodenum is the opening of the duct by which the *bile*, formed in the liver, enters the gut. The bile is a complex fluid, containing three main types of substance. There are in the first place *pigments*

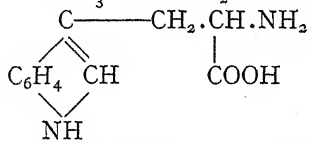
(bilirubin and biliverdin), which are formed in the liver and elsewhere by the breakdown of the red pigment hæmoglobin of the blood. These pigments are probably only waste-products to be cast out. That is also, most probably, the fate of the *cholesterol* in the bile, for bile is the only fluid of the body in which cholesterol is at all soluble—and even here it tends to form hard, solid masses (gall-stones). Thirdly, the bile contains salts of two complex nitrogenous acids (taurocholic and glycocholic acid). The bile contains no digestive enzymes, but it acts as a natural laxative and disinfectant; and it aids in a most remarkable degree the action of the pancreatic enzymes, especially of the fat-splitting steapsin. The salts of the bile combine with the fatty acids set free, and thus form compounds which, unlike the fatty acids themselves, can be absorbed by the cells of the intestine and taken into the body. Thus the bile salts are not lost to the body, but go through a regular cycle, passing into the gut only for a time.

In the intestine the digested food (chyme) receives no further active juices, except small amounts of the enzyme erepsin, which is also present in duodenal secretion, and indeed in almost all cells. This continues the resolution of proteins into amino-acids, and small amounts of enzymes of lesser importance. By this time the carbohydrates are all converted into glucose, the fats into glycerol and fatty acids, and the proteins into amino-acids (with the exception of such members of these groups as may be indigestible); and it is in the small intestine that the absorption of these simplified products takes place. However, the food-materials may yet be further and very considerably altered by the action of the bacteria which are present in enormous and increasing numbers from the duodenum onwards, and above all in the large intestine. The great majority of these are fortunately harmless, and may even do a certain amount of service in digesting such materials as the complex carbohydrate cellulose, which resists all vertebrate digestive juices; but they tend to form large amounts of gases (carbon dioxide, methane, sulphuretted hydrogen), besides evil-smelling (scatol, indol) or even dangerously poisonous (ptomaine) compounds. If their growth is encouraged by irregular habits or unsuitable diet, disease-causing bacteria (of colitis, dysentery, paratyphoid, and so on) may profit by the favourable conditions. The number of these organisms normally present is inconceivably great; five million million may be eliminated daily.

Relatively little is known in regard to the absorption of substances from the intestine into its lining cells, and eventually into the blood. It is one of the most difficult aspects of the difficult problem of cell-permeability which we have discussed elsewhere. It will be enough to say that the amino-acids and simple sugars enter the cells and thence pass into the capillaries and are carried to the

liver, without being chemically changed in any way. The fatty acids and glycerol absorbed, however, have a very different fate; they immediately combine with one another to form fats in the lining cells of the intestinal wall, from which they are discharged, not into the blood stream, but into special channels (lacteals) in the form of a milky emulsion (chyle). These lacteals lead to the thoracic duct and finally are connected with the blood-stream at a point near the left shoulder in man.

4. Intermediate Metabolism.—Of the amino-acids absorbed from the intestine, a large part is used by the body as a source of energy, while a smaller part is built up into proteins. Very little is known of this latter process, but a short digression on the nature of proteins and their occurrence in the body may be of service here. Emil Fischer showed conclusively that the essential feature of the structure of the enormous protein molecule was a long chain of amino-acids, such as—

Glycine $CH_2.NH_2—COOH$
Alanine $CH_3—CH.NH_2—COOH$
Tryptophane 
Tyrosine $C_6H_4.CH—CH_2—CH.NH_2—COOH$
Cysteine $CH_2.SH—CH.NH_2—COOH$

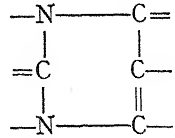
and so on. When these are united to form chains in a protein molecule, each amino-acid loses the elements of water, one hydrogen atom from its $—NH_2$ (amino) group, and one hydrogen and one oxygen from its —COOH (carboxyl) group, so that a glycine molecule within a protein has the structure

$$\begin{array}{l} \quad CH_2.NH— \\ —CO \end{array}$$

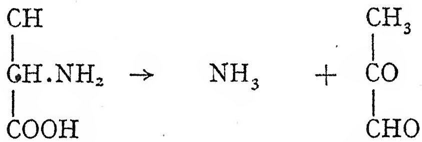
being united to other amino-acids on either hand. Hence when proteins are digested, for each molecule of amino-acid set free one molecule of water must be incorporated into its structure; such a process of splitting is called hydrolysis.

Many of the proteins of the body appear to consist solely of amino-acids, such as the albumin and globulin of the blood serum and the elastin of elastic fibres. But the proteins very often unite with other types of substance, and examples of such "conjugated" proteins are the red hæmoglobin of the blood, the casein of milk, and the vitellin of egg-yolk, which contain phosphorus, mucin (used throughout the body as a lubricating agent), which contains sugar,

and the nucleoproteins. In this last case the protein is united with the complex nucleic acid, which contains phosphoric acid, a sugar, and four different nitrogenous substances, built out of the ring—

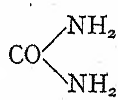


Much more is known of the metabolism of the absorbed amino-acids that are destined to yield energy, though even here a great deal of uncertainty remains. The first change which they undergo is that they are deaminated, that is, the $-NH_2$ or amino group is split off to form ammonia (NH_3), while the rest, containing carbon, hydrogen, and oxygen only, is oxidised to carbon dioxide and water, yielding energy. It is possible to imitate these reactions in part at least in the laboratory, for example:



Alanine → Ammonia + Pyruvic aldehyde

Pyruvic aldehyde is readily oxidised to pyruvic acid, an important substance (CH_3—CO—COOH), which in turn yields carbon dioxide and water by way of acetaldehyde. It is not very certain whether this process of deamination is carried out in the liver only, or in all organs of the body, nor is it certain whether the liver is the chief site of the transformation which changes the harmful ammonia into the innocuous urea,



which is one of the chief waste products of the body.

The sugars are oxidised, for the most part, in a very similar way, since they readily yield lactic acid and pyruvic acid; but some fraction is possibly diverted in other directions. Less is known of the oxidation of the fats, but it probably follows a similar course.

Two important features remain to be considered, the first being the question of storage. Carbohydrate is stored in large quantities in the liver and the muscles, in the form of glycogen, a complex substance similar to starch, while the existence of stores or depots of fat is familiar to everyone. The second point is that the animal body has a great power of converting one type of substance into

another. This depends largely on the fact that the reactions which yield pyruvic acid are to a large extent reversible, so that the body can form alanine from pyruvic acid and ammonia, as well as carrying out the reverse change; and fats may also be formed from the same substance. It is easy to see, then, that fats can be formed from either proteins or carbohydrates, by way of pyruvic acid.

5. The Blood and the Transport of Gases.—As is well known, one function of the blood is to transport food materials from the wall of the intestine to the tissues in which they are used up, or stored, or transformed into other substances. A second function is to transport gases—oxygen from the lungs to the tissues, and carbon dioxide from the tissues to the lungs. But before this can be explained it is necessary to interpolate a description of the blood itself.

The blood consists of a pale yellow, watery fluid, the plasma, in which are suspended enormous numbers of single cells—so many that they make up nearly half of the whole volume of the blood, and there may be five million in one cubic millimetre, perhaps thirty billion in the whole human body. The great majority of these cells are red blood corpuscles, minute discs without nuclei, which contain the red pigment (hæmoglobin) of the blood; there are also white corpuscles (leucocytes) of various kinds, two or three to every thousand of the red cells, and apparently important mainly through the power which most of them possess of engulfing foreign bodies, for example, bacteria. This property (phagocytosis), which is separately discussed, is also shown by certain fixed cells, for example, in the liver; and in many Invertebrates particles of food are taken up by such cells and digested within them. Little, however, is known of the chemistry of the leucocytes, since they are so greatly outnumbered by the red cells of the blood. It is on these red cells that the transport of gases mainly depends.

Another property of the blood may be noticed here, and that is its power of clotting or coagulating when it escapes through a wound in the blood-vessels. This is by no means merely a question of "drying up", but a very complex affair not yet thoroughly unravelled. By some interaction of unknown substances, a protein in the fluid plasma of the blood becomes transformed into a stringy solid (fibrin), in which the cells of the blood become entangled to form a clot. A part is also played by certain elements of the blood not yet mentioned, the platelets, extremely small solid bodies with little discernible structure and of very obscure function.

Oxygen, like other gases, dissolves to some extent in water or any aqueous solution, to an amount depending on various factors, such as temperature, and more particularly on the *pressure* of the oxygen. It is known to everyone that under standard conditions the pressure of the atmosphere is 15 pounds per square inch, corresponding to a definite height of the barometer (760 millimetres of mercury).

Since oxygen makes up 21 per cent. of the air, the *partial pressure* or *tension* of oxygen under these conditions is 21 per cent. of 760, i.e. 160 millimetres of mercury. If the total atmospheric pressure is increased, or the amount of oxygen in the atmosphere is increased, then in either case the tension of oxygen is increased and a larger amount will dissolve in water. The amount dissolved is always in equilibrium with the atmosphere above it, so that it is possible also to speak of the tension of the *dissolved* oxygen. There are, of course, certain substances which combine with oxygen (such as pyrogallol) to form compounds from which the gaseous oxygen cannot be obtained again readily; but there are also compounds which combine loosely with oxygen to an extent depending on the oxygen tension; and one of these is hæmoglobin, the red pigment of the blood corpuscles. The hæmoglobin combines with oxygen when the blood is passing through the lungs, where the oxygen tension is relatively high, and gives up the oxygen again as the blood passes through the tissues, where the oxygen tension is low. The compound which the pigment forms with oxygen is called oxyhæmoglobin; and it is found that it contains two added-on atoms of oxygen for every atom of iron (there are probably four atoms of iron in every molecule of hæmoglobin, but this is uncertain), so that the contraction HbO_2 is often used for oxyhæmoglobin.

Carbon dioxide is carried by the blood in a somewhat similar way, that is to say, it can all be removed from blood by sufficiently lowering the carbon dioxide tension of the atmosphere in contact with it—in a vacuum, for example; but it can also be driven out of blood by adding strong acids. The latter property is shown also by solutions of sodium bicarbonate ($NaHCO_3$), and indeed the plasma does contain inorganic bicarbonates which aid in the transport of CO_2. The carbon dioxide thus carried is called the "alkali reserve" of the blood. This, however, is greater than might at first appear, because of a curious series of reactions which go on. Of these the first merely expresses the passing of the gas into solution:

$$CO_2 + H_2O = H_2CO_3$$

Then follows the reaction of the carbonic acid with the sodium chloride of the plasma:

$$H_2CO_3 + NaCl = NaHCO_3 + HCl$$

but as hydrochloric is a strong and carbonic a very weak acid, this reaction would take place only to a very slight degree, if it were not that the hydrochloric acid, as soon as it is formed, tends to pass into the corpuscles (where it is neutralised). This mechanism—called the "chloride shift" by some and the "ionic interchange" by others—allows the plasma to carry more carbon dioxide than it could if the corpuscles were not there to take up the hydrochloric

acid. Lastly, carbon dioxide is also carried, to a considerable extent, by the hæmoglobin in the corpuscles themselves.

A problem which has yet to be considered is the balance maintained by the blood acidity and alkalinity. This is important; in the first place because it is probably an increase in acidity of the blood which causes the "respiratory centre" of the brain to send nervous messages to the lungs, commanding them to expand and draw in more air; this increased acidity being due to an increase of the amount of free carbon dioxide in the blood. It should also be mentioned that the blood has a remarkable "buffer" action, or power of counteracting any changes in its alkalinity, which, though varying in the cycle between venous and arterial blood, remains singularly constant at any one point in the circulation.

We find, then, as L. J. Henderson has shown, that the blood is a complex physico-chemical system, in which there are at least six variable factors: the oxygen tension, the carbon dioxide tension, the amount of combined oxygen (oxyhæmoglobin), the amount of combined carbon dioxide (in various forms), the distribution of chlorides between corpuscles and plasma, and the alkalinity or hydrogen-ion-concentration of the plasma. All these factors vary together; and if any two are arbitrarily fixed, the other four can be accurately calculated, according to definite laws of physico-chemical equilibria.

6. Salts of the Blood and Salts of the Sea.—Of much biological interest is the correspondence between the salts of the blood and the salts of the sea. Both in the nature of these salts and in their relative proportions there is a remarkable likeness between blood and sea-water, as has been worked out by Quinton and Macallum. The correspondence is greater when account is taken of the change in the composition of the sea—towards increased salinity—since blood-possessing animals were first evolved in Cambrian times. To start with, the specific gravity of the two fluids was probably the same. "We cannot shake off the lien the past has upon us; when our head throbs we may hear the primeval ocean breaking on the Cambrian shore."

7. Immunity.—One of the most remarkable properties of the blood is the power the serum has of forming specific substances to combine with foreign substances introduced into the body. Substances which provoke this reaction are called "antigens". Any soluble protein not normally present in the blood may act as an antigen; but it is probable that only proteins can do so. The substance which the serum forms in response to the introduction of an antigen is called an anti-body, and the reaction between antigen and anti-body may be any one of various different types. If the antigen is soluble, it will be *precipitated* by the anti-body. If

it is not soluble but in the form of visible particles, these will be *agglutinated* together in heavy clumps; this may also be the fate of foreign cells, bacteria, for example, but cells or solid particles may also be *dissolved* by the anti-body in the process called *lysis*. In the case of lysis, however, the anti-body in the serum does not act alone, but requires also the presence of an unknown substance already present in serum called alexin or complement. Lastly, the case in which the antigen is a poison (*toxin*), which is by no means necessarily the case, must be considered; here the effect of the anti-body (anti-toxin) is to *neutralise* the poison.

It is possible that the anti-toxins are rather different in their nature from other anti-bodies; but as the chemical nature of all these substances is as yet unknown—they have never been obtained in anything approaching a pure state—it is difficult to make definite statements. It is probable that anti-bodies are proteins, but even this is not securely established; and the mode and site of their formation are equally obscure. It should be noticed that in some cases the blood may contain *natural* anti-bodies capable of reacting with antigens which have never been introduced, whilst those formed after the injection of the antigen (immunising) are called *immune* anti-bodies.

One of the most striking features of these reactions is their great specificity. A rabbit may be immunised to human blood, so that when the rabbit's serum is mixed with a minute quantity of human serum it will give a precipitate; but with serum from an anthropoid ape it will give no precipitate, or only a slight one. In this way proteins can be identified with greater certainty than by chemical methods, and in extremely minute quantities: and since the specificity of the reactions is quantitative rather than qualitative, the fact that two proteins, though not identical, are related, may also be demonstrated; for it seems reasonable to suppose that proteins differing in their "immunity" reactions must also differ chemically, although it may be hard to establish the latter point in particular cases. The important fact is that although we know so little of the reacting substances, there seems little doubt that the reactions themselves are exactly analogous to reactions familiar in colloid chemistry, such as the precipitation of colloids by removing the electric charge on the particles. This is true even in the more difficult case of lysis, with its intervening "complement", which is apparently a complex of proteins, occurring in all serums naturally, and not specific. That is to say, it is capable of playing its part in *any* lytic reaction.

As immunity has a familiar Natural History aspect as well as a deep physiological interest, we may discuss it less technically from the wider point of view.

It is a well-known fact of natural history that a hedgehog may

be bitten by an adder without suffering evil effects so far as one can see. This has been corroborated experimentally, and it appears that a hedgehog is not affected by an injection of poison many times stronger than the fatal dose for a rabbit. The hedgehog has natural immunity to the venom of vipers.

But what does this immunity mean? The first step towards an answer is not difficult, and has been well worked out for the attractive carnivores known as the ichneumon and the mongoose, both of which are inveterate enemies of snakes, and enjoy the same natural immunity as the hedgehog. If some cobra's poison be mixed with mongoose's blood, and if the fluid or serum be injected under a rabbit's skin, nothing happens; but an injection of the same amount of poison without mongoose's serum is immediately fatal.

Counteracting Substance.—The same is true for the hedgehog and adder's poison. Evidently, then, there is some substance or quality naturally present in the blood of mongoose and hedgehog which is able to counteract, neutralise, or somehow take the edge off snake-toxins.

The hedgehog, the ichneumon, and the mongoose can withstand large injections of poisons; thus the ichneumon can successfully counteract six times the dose that is fatal to a rabbit. But in all cases there is, naturally enough, a limit beyond which the poison is fatal. A few other mammals are known to be immune to snake-poison; thus the American opossum is not affected by the bite of a rattlesnake, and the cat has a high degree of immunity to the poison of vipers. A few mammals have a distinct but slight insusceptibility to snake-poison; most have none at all.

The cobra's poison has no effect on other cobras of the same species, and this is a general rule. But when a venomous snake bites a relative that belongs to a different species, the result may be fatal, as is generally the case with different kinds of vipers. A cobra is not much affected by viper's poison, while the viper readily succumbs to a cobra's! All this shows how *specific* the immunity may be. There are many peculiarities of this sort which do not readily find explanation at present.

Artificial Immunity.—The immunity which is so well illustrated by the hedgehog and the mongoose is *natural* immunity; but the same quality of insusceptibility may be more or less artificially *acquired*. One method is to begin by injecting minute doses of the poison and continue with gradual increase in quantity. The blood gets into a condition of resistance or insusceptibility, neutralising doses which would otherwise have been fatal. Thus a man may be immunised to snake-bite. The theory is that the blood is able to prepare a garrison of "anti-toxins" or "anti-bodies"—what's in a name when we do not know what they are, if they are?—sufficient to withstand a strong invasion of toxins. On the same principle, an

injection of vaccine microbes will enable the organism to withstand the intrusion of smallpox microbes.

The other method is to inject a serum preparation of the blood of an animal that has been immunised by graduated direct doses of the poison, or by non-fatal attacks of the virulent microbes. Some animal, such as a horse, is rendered immune, and its serum, abounding in anti-toxins according to the theory, is injected into another organism. This method is less drastic than the other, yet very effective. It is often used as a protection against a probable poisoning, whether by snake-bite or by some virulent microbe, as well as an antidote after the introduction of the poison has taken place. It might be thought that it would be better still, in the case of snake-bite, to utilise the serum of a *naturally* immune animal, such as the hedgehog or the mongoose. But there is only a small quantity of the anti-toxin present in the blood of these naturally immune animals; the counteractive effect does not last long; and there are positive disadvantages in the use of the serum so obtained.

IMMUNISATION BY DISEASE.—Another form of immunity is very familiar—namely, that which follows recovery from a disease. The individual is more or less protected against taking the disease a second time. The immunity may last for many years in the case of smallpox, but there are records of two or even three attacks; it may be strong, as in the case of scarlet fever, measles, and mumps; it may be transient, as in diphtheria. There are rare cases, such as pneumonia: here the immunity is at most very temporary; where, indeed, susceptibility to the disease appears to be increased, not decreased.

There is evidence in some instances that an artificially immunised rabbit or guinea-pig has young ones which are born immune. The same is asserted in regard to smallpox, that the immunised human mother may confer immunity on her offspring; but it is difficult to prove this satisfactorily. If it occurs, it may be due to specific anti-toxins passing via the placenta from the blood of the mother.

When there is evidence of immunity as a racial character—as in the case of negroes, who are relatively immune to yellow fever and malaria, or in the case of Algerian sheep, which are relatively immune to splenic fever or anthrax—the explanation is probably that a constitutional variation, like the hedgehog's, arising apart from injection or other poisoning, has become hereditary, whereas those members of the stock who did not vary in the direction of immunity would be gradually eliminated.

FIELD FOR RESEARCH.—For many years Ehrlich's "side-chain" theory of immunity was greatly admired, and it has been provocative of useful investigation. But it is no longer in favour; and many authorities would not at present go farther than say that immunity in animals, whether natural or acquired, implies a subtle peculiarity

in the complex colloidal mixture that we call the serum of the blood, such that it looks as if anti-toxins counteracted toxins. Yet, all theory apart, immunisation has already done much for the relief of man's estate.

8. ANAPHYLAXIS.—Closely related to these phenomena of immunity, though at first sight in disharmony with them, is "anaphylaxis". If an animal is first treated with a small dose of antigen, so that anti-bodies are formed, and some ten days are then allowed to elapse before introducing a further and perhaps very small amount of the same antigen, "anaphylactic shock" immediately supervenes. The symptoms of this vary in different animals, from violent and rapidly fatal asphyxial convulsions in guinea-pigs to much milder disorders—often only a severe rash—in man. These dramatic results can be shown to follow the injection in two doses of an amount of foreign (and possibly quite harmless) protein, much less than that which the animal could easily survive in a single dose.

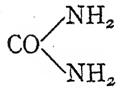
It seems likely that in anaphylaxis the reaction between antigen and the anti-body formed by the first injection takes place, not in the blood, but in the cells of the tissues. For example, if suitable smooth-muscle tissues from a "sensitised" animal are treated, under the proper conditions, with a small dose of the antigen, a violent contraction will take place. Specificity is very marked in this case also: it must be the same antigen that is introduced before and after sensitisation. It is also clear that here again we are dealing with a chemical reaction; since a sensitised muscle preparation that has once responded to a second dose of antigen by violent contractions will not again respond to a third dose: the anti-body that was in the muscle cells has been used up. The reaction produced, it should be noticed, is the same in any one species of animal, whatever the antigen selected is.

As Dale, one of the leading workers in this field, has pointed out, we have in anaphylaxis "the physiological response of an animal in a certain phase of immunity to the artificial test which we impose", and in no sense a negation of the practical defensive protection that immunity confers on the body.

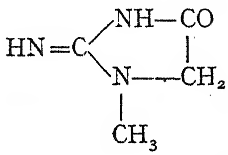
9. EXCRETION.—As obvious end-products of the reactions of metabolism we must reckon (1) carbon dioxide, which is volatile and escapes from the body in the expired air, and (2) water, which escapes from the lungs, from the skin, into the alimentary canal and through the kidneys. There remain, however, (3) waste-products containing the elements nitrogen, sulphur, and phosphorus, which are not volatile, and are got rid of chiefly through the kidneys. Although the duodenum, the colon, and the liver may have an excretory function, their importance in this connection does not seem to be very great.

According to Folin's theory of protein metabolism, already referred to, the amino or $- NH_2$ groups of amino-acids are transformed into ammonia, and this ammonia is converted into urea, which in man is the principal nitrogenous waste-product. Within eight or ten hours of a meal, nearly the whole of the nitrogen in the protein consumed is excreted in the form of urea. This urea, whose nitrogen is directly derived from the amino-acids of the food, is called *exogenous*; but there is also a much smaller excretion of *endogenous* urea, due to the break-up of the proteins which actually form part of the living tissues, and are always suffering a certain amount of wear and tear.

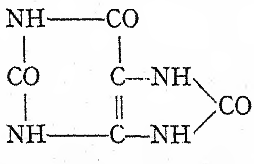
Urea, with its formula



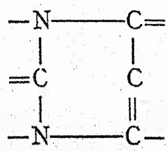
is the simplest and in man the most important in amount of the nitrogenous waste-products, but it is by no means the only one. Thus, of undoubted importance, though somewhat puzzling in origin, is creatinine,



which appears to be almost entirely *endogenous*, since the amount excreted seems almost wholly independent of the amount of nitrogen in the food. Creatine, a closely related product, occurs in considerable amount in the muscles (which always contain various nitrogenous "extractives" of this type), yet it is by no means certain that the creatinine of the urine is derived from this. Another important waste-product, notably in Invertebrates, is uric acid,



of which part is derived from the food and part is derived from the breakdown of the nucleo-proteins, which, as we have seen, contain substances of the pyrimidine type. The pyrimidine ring



forms part of the uric acid molecule, as will be seen on comparing the formulæ. Nucleic acid also contains substances more closely allied to uric acid, having the same double-ring structure (purines). It may be mentioned that the excreted products are very different in different classes of animals; in most mammals uric acid is further oxidised to allantoin, while in birds urea is actually transformed into uric acid, which becomes the chief nitrogenous waste-product.

The sulphur-containing waste-products are also important, and may also be distinguished as "endogenous" and "exogenous". The chief source of sulphur is the amino-acid cystein, which contains a sulfhydryl or — SH group. The liver has the power of oxidising this to a sulphate or — SO_4 group, and inorganic sulphates are excreted in the urine. These substances have the property of combining with various aromatic substances (phenol, indole) formed by the intestinal bacteria and harmful to the body, whereas the ethereal sulphates formed by this reaction, such as potassium indoxyl sulphate,

$$SO_2\begin{array}{l} \diagup O.C_8H_6N \\ \diagdown O.K \end{array}$$

are harmless. Such protective syntheses are undoubtedly valuable: another example is the combination between benzoic acid and the amino-acid glycine to form the harmless hippuric acid, a reaction that is known to go on in the kidney itself.

All the sulphur-containing compounds absorbed by the intestine and most of those liberated in the breakdown of tissue proteins will pass through the liver and be largely converted to sulphates; but a fraction of the endogenous sulphur will reach the kidney without passing the liver, and is excreted in the reduced form as "neutral sulphur" compounds of somewhat obscure composition. Phosphorus, like sulphur, is both endogenous and exogenous, and is excreted in the form of inorganic phosphates.

We may now examine a little more closely the action of the kidney, the organ which separates out these waste-products and discharges them from the body. In its simplest aspect a kidney need be little more than a filter, which allows the water and all dissolved substances, salts and waste-products alike, to leave the blood, but prevents the colloids from passing through. In marine animals which have no need to economise either water or salts, such an arrangement works very well; but in the higher vertebrates the kidney is much more specialised in its action, so as to retain part of the water and salts.

The kidney consists of a large number of minute tubules which form the internal or medullary part of the organ. They unite inwardly to discharge the excreted fluid into the ureter, while outwardly, in

the cortex of the kidney, they end in tiny filters (called glomeruli). The theory of the action of these structures is still disputable, but Cushny's account of it is the most complete and satisfactory. According to this view, the glomeruli are simple filters of the type suggested above, but the tubules in the kidney medulla reabsorb water, salts, and useful dissolved substances from the filtrate, and retain them within the body, while they refuse to absorb waste-products. The filtrate passing the glomeruli, then, has the composition of the blood minus its colloids—that is, much water, various salts, some food materials (glucose), and a relatively small amount of various waste-products. The tubules tend to absorb from this filtrate a fluid having the composition of the *useful* part of *normal* blood, containing no waste-products. All the waste-products which pass the glomerulus therefore pass the tubules also and are discharged. But if any of the useful constituents of blood be present in too great amount, whether water, or salts, or glucose, then the excess will not be absorbed by the tubules (which take out only the quantity contained in *normal* blood), but will be discharged. So that when water or salts or glucose pass a certain limit in the blood, and therefore in the glomerular filtrate, the excess is got rid of from the body; they are therefore spoken of as "threshold" substances, whereas the waste-products like urea are excreted however little may be present, and are called "No-threshold" bodies.

The total action of the kidney, then, is to remove from the blood all the waste-products, and the excess of the "threshold" substances such as water, salts, and glucose (the latter only attaining the threshold in experimental conditions, or in the disease of diabetes). It should be noticed that the urine is a more concentrated fluid than the blood, and therefore the kidney performs actual work and expends energy, since work must be done to concentrate a fluid. The kidney, of course, is not a perfect organ; it allows traces of useful substances to escape; especially in disordered conditions, to which, unfortunately, it is only too subject.

Animal Heat.—Animals obviously expend energy in moving; birds and mammals usually have to expend energy to maintain their body temperature at its constant level; all living cells expend energy in many subtler ways. The chief subjects of physiological study are the sources of this energy; the means by which it is made available; the ways in which it is expended, and the control of this expenditure. The analogy between an animal and a candle, which also expends energy and which also "uses up" air and "dies" in a confined space, was thoroughly appreciated in the early eighteenth century; but it was not known what the candle did to the air in which it burned, still less how animals transformed the air they breathed.

The answer to both questions was found by Lavoisier in 1776 and the following year. He showed, simply and convincingly, that about one-fifth of the volume of ordinary air consisted of a gas to which he gave the name "oxygen", and which had the power of combining with metals, or with the carbon of "organic" substances, or with hydrogen and many other substances, when they were sufficiently heated in air. With metals oxygen forms earthy oxides, such as rust; with hydrogen it forms water; with carbon it forms a gas, the "fixed air" of earlier chemists, which Lavoisier recognised as carbon dioxide. In the burning of a candle, then, the oxygen of the air combined with the carbon of the wax or tallow to form carbon dioxide, and in this process energy was set free, to appear as light and heat. He then showed that mice also used up the oxygen of the air they breathed, and produced carbon dioxide, and he concluded that in the animal body a slow combustion took place, the carbon of the organic materials of the body—continually renewed by the food—combining with the oxygen of the air, with formation of carbon dioxide and liberation of energy for the needs of the body. Where this combustion took place Lavoisier did not know; for some time it was commonly thought to take place in the lungs, then in the blood, and at last it was established that it takes place in every cell in the body, but most vigorously in the muscles.

To Lavoisier and his contemporaries these theories seemed novel and hazardous; and it was necessary to prove their validity by actual measurement, as accurate as the technique of the time permitted. With the help of the great physicist Laplace, he constructed a "calorimeter"—that is, an apparatus for measuring the amount of heat given off by an animal or in a given chemical reaction. This consisted of a double-walled can, with ice packed in between the walls to prevent heat entering from outside—since this was long before the invention of the vacuum flask. The interior of the apparatus contained a cage in which a guinea-pig was placed, and round the cage more ice was packed; the water which was formed by the melting of this ice was collected and weighed, and served as a measure of the amount of heat given off by the guinea-pig during the experiment: for instance, it melted 40 grams of ice in an hour. Before or after the experiment the amount of carbon dioxide produced by the animal was measured, and found to be a third of a gram per hour; and Lavoisier and Laplace determined that the burning of carbon at this rate should set free enough heat to melt $32\frac{1}{2}$ grams of ice in an hour. The agreement between the two figures (40 and $32\frac{1}{2}$) was not very good, but it was suggestive, and might perhaps become closer if possible sources of error were tracked down. First of all, it had to be remembered that the animal was warm when put into the ice-chamber; secondly, it was certain that combinations of hydrogen with oxygen in the animal's body also

yielded heat; thirdly, it was possible that the animal produced carbon dioxide more rapidly when it was in the ice-chamber than when it was at a comfortable temperature, during the determination. When all these points were considered and allowed for, the figures as corrected were in sufficiently good agreement for Lavoisier to be sure that he had satisfactorily accounted for the production of animal heat; and more accurate repetitions of this experiment since his day have amply confirmed him.

The last of the three points taken into consideration in correcting the gross results led Lavoisier to a further series of experiments which were arrested by his execution, but which were of the greatest importance. He showed that a man, just as much as a guinea-pig, did use up more oxygen and set free more carbon dioxide at a low temperature than at a temperature corresponding to that of the body—naturally, since the body temperature has to be kept up in spite of increased loss of heat; further, that a man during the digestion of a meal used up more oxygen than he did when fasting —thus proving that work was done during digestion; and finally, that a man doing hard work, in lifting a weight, used up oxygen some three times as fast as a man resting.

THE COST OF LIVING.—Experiments on the same principle as Lavoisier's are constantly being made in laboratories all over the world, with costly but accurate apparatus, on a larger scale. There are automatic machines which record the amount of carbon dioxide in the air; calorimeters are built as large as small rooms, in which a man can rest or perform muscular work, as the experiment demands. The object of the experiments has changed too: it is no longer necessary to seek proof of Lavoisier's idea, that the animal body is comparable to a machine in its intake and output of energy, and obeys the same physical laws. But the method has proved a most valuable one in the investigation of physiological problems, and also in medical diagnosis.

In either case, special emphasis is laid on the problem of determining the physiological cost of living, that is to say, the amount of energy which is given out by the body—and, if accounts are to balance, must be returned to the body in the form of food—when no unnecessary work is being performed, and the body is merely keeping itself alive. The beating of the heart, the movements of breathing, the maintenance of the normal temperature in spite of loss from the surface—these processes, and doubtless more subtle ones also, demand energy, but apart from these absolute rest is aimed at. Under such conditions, the energy output of the body at rest, the "basal metabolism" as it is called, has been determined for thousands of individuals.

It is possible to determine this value in many ways—by oxygen consumption, by carbon dioxide formation, by heat production, by

change in body weight, and so on, for from any one the others can be calculated more or less accurately. But most emphasis is placed on the production of heat, as the most direct measurement of energy output and basal metabolism is usually expressed in terms of heat production. The unit is the Calorie, which is the amount of heat required to raise the temperature of a kilogram (nearly a quart) of water from 15° Centigrade to 16°, or, roughly, a third of an ounce of water from freezing-point to boiling-point. An average figure for the basal metabolism of a man is 2,000 Calories a day, which represents an output of energy of about one-seventh of a horse-power. If really hard muscular work is done, the daily output of energy may rise to three times that figure or more.

Naturally the figure of the basal metabolism varies a great deal from one person to another; it bears some relation to the weight of the body, but more to the area of the surface of the body—not, unfortunately, very easy to determine directly. The reason is that the amount of heat lost from the body depends on the amount of surface. In the same way, when different kinds of animals are compared, it is found that smaller animals have usually a higher relative basal metabolism than large ones, because their surface-to-weight ratio is larger. It is not always easy to obtain good figures for animals, however, both because it is not always possible to get them to rest during the experiment, and also because cold-blooded animals have not such a delicately poised physiological balance as mammals and birds; in their case basal metabolism has not such a definite, reproducible value, but may depend on their state of nutrition and so forth, so that only average values can be obtained.

In basal metabolism determinations the subject of the experiment is at rest, and starving. But by simple variations, using the same method, it is possible to determine the cost of various sorts of work, including the work done in keeping warm at various temperatures of the air, the work done in maintaining the raised temperature of fevers, the work done in digestion, and the cost, in terms of work, of growth. The value of different kinds of food as sources of energy, and the effect of stimulants and other drugs, may also be investigated in this way.

The chief function of the thyroid gland is to regulate the level of metabolism, and whenever a disorder of this gland is suspected, so that it may be functioning too much or too little, basal metabolism determinations are of great value in identifying the condition and watching the progress of the cure. When the active principle of the gland (thyroxin) was prepared synthetically, one of the first tests applied to it was to see whether it raised the basal metabolism of a healthy individual as markedly as an extract from the natural gland does.

FERMENTATION

THE YEAST-PLANTS.—In connection with fermentation something must be said of the common yeasts. One is usually told that yeasts are fungi; but even if this is a technically accurate classification, it is not very enlightening. Just as there is much to be said for separating off bacteria from all other creatures as a line of life by themselves, a distinct phylum or group, so the yeasts should be separated out of the mob of fungi—moulds and mildews, toadstools and mushrooms—and kept by themselves. They are minute unicellular plants that have the power of setting up the process of fermentation, which is so important in making both bread and beer.

The use of yeast in changing sugars into alcohol and carbon dioxide gas goes back for at least four thousand years, and some people associate the discovery with the name of Noah. For many centuries, at any rate, it has been well known that the "barm" or "leaven" was indispensable in the brewing or the baking, yet its rank as a living creature was not realised till less than a hundred years ago. It is true that in 1680 Leeuwenhoek, a most extraordinary observer, sent a paper to the Royal Society entitled "De Fermento Cereviseæ", in which he described the small ovoid globules of yeast, each about one-three-thousandth of an inch in diameter; but he did not recognise their plant nature. As Mr. A. Chaston Chapman recently pointed out in his presidential address to the Royal Microscopical Society, it was not till about 1837 that "the true nature of the yeast organism was definitely and independently discovered by three observers—Cagniard de Latour, Schwann, and Kützing. These observers recognised that yeast is composed of a vast number of small transparent globules which reproduce by budding, and which consist of a cell wall with granular contents." About two years afterwards Schwann observed that the yeast-plant can also multiply by forming internal spores. By and by came the detection of vacuoles and nucleus, granules and threads, in the well-equipped microcosmic laboratory.

The oldest notion of yeast fermentation was that the yeast is a very active something with particles in vigorous motion, and that this mobility is somehow imparted to the more sluggish particles of the substance that is fermented. Second, there was Liebig's chemical theory (1839) that oxidation of nitrogenous matter in the yeast brings about contact-decomposition in the molecules of the fermentable matter in which the yeast is working. Thirdly, this was modified by Pasteur's insistence (1856) that the formation of the various fermentation products is directly associated with the life activity of the yeast-plant.

But fourthly, there came in 1897 Büchner's important discovery

that a ferment or enzyme secreted by the yeast—made by it in its one-three-thousandth of an inch laboratory—can bring about fermentation without there being any living yeast cells in the substance that is fermented—that is, the extract of the yeast will do the same work as the living yeast.

Beyond this, however, investigators are pressing, and bringing us back again to Pasteur; for they have proof that the living yeast-plants work far better than the non-living yeast juice. The fermentation induced by the living organism is more rapid and also more regular—that is to say, less liable to be disturbed by extraneous influences. Another line of inquiry concerns the tracking back of the ferment (zymase) to the probable parent substance (certain definite granules) formed in the living matter of the yeast cell. It is indeed usual in ferment-making cells that the ferment should first appear in a masked or inactive form called zymogen. But we do not yet know how the ferment achieves what it does.

From the general natural history point of view the salient fact is that the yeast-plant feeds on the sugar. It is on the strength of the sugar that it multiplies prodigiously by budding, quickly leavening the whole lump. But it cannot utilize the sugar as a source of energy by oxidation or combustion as we, for instance, do; it utilises it in a wasteful way by fermentation, which leaves about 95 per cent. in the form of alcohol. The carbon dioxide liberated in the fermentative change makes the bread "light", and it accumulates in large quantities in the process of brewing. As a heavy gas it sinks in air, and we used to read in old books that it would put out a candle lowered into the emptied vat, and so make it dangerous or even fatal to a workman descending into it.

Of great practical importance is the modern precision which has made it possible to distinguish many different kinds of yeast-plant. An expert like Mr. Chapman separates out not merely species, but genera, which differ from one another in shape and size, in their mode of multiplying, and in the way they work. The brewer's and distiller's yeast, that has been cultivated for so long, is probably one species (*Saccharomyces cerevisecæ*), but of this there are many races and varieties, differing in the rapidity with which they bring about fermentation and in the flavour of their products. It was a great step when Hansen, in 1879, showed how it was practicable to isolate a single yeast cell and thus start a pure culture. It must be kept in mind that there are many "wild" yeasts, such as those that wait in the vineyard soil till the grapes are ripe, and it is very plain that in industrial processes the microscope must guard the door against intruders which are unsuitable for the particular end in view. Science is always eliminating chance.

FERMENTS.—Man's knowledge of ferments is very modern, but his knowledge of fermenting is very ancient. Vines were cultivated

and wine was made by 3500 B.C., if not much earlier, and wine-making means familiarity with fermentation. The juice of the grape, squeezed out in the winepress and left to itself, soon begins to bubble and froth. It gives off carbonic acid gas and "boils up", and this boiling up is what the word "ferment" refers to. It has the same root as the words "fervent" or "perfervid". The outcome of the boiling up is that the sugar of the grape juice is changed into the alcohol of the wine; and we know what was hidden from the ancients, that the agents in the change are yeast cells. These are always to be found in the soil of the vineyard, whence they are carried by insects on to the fruit, which they enter through minute wounds. There are always sufficient infected grapes to start the fermentation in the vat, but nowadays the careful maker of wine does not leave things to chance nor to stray "wild yeasts".

There are other fermentations of very ancient origin, such as the making of vinegar out of weak alcohol exposed to air. This is a discovery that would readily be made by chance in connection with wine-making, for dilute wine left exposed soon turns into vinegar. In the course of a few days a slimy mass appears on the surface, and we now know that this so-called "mother of vinegar" consists of countless "acetic acid bacteria" entangled in a sort of thin jelly which they produce. In various countries from very ancient times drinks have been made from different kinds of milk by means of "lactic acid bacteria", sometimes helped by yeasts. Of course the ancients did not know about bacteria or yeasts, but it is interesting to find that in certain cases they added "something" to what was to be fermented, just as they added "leaven" to the dough that was to be baked. In making the milk drink called "Kefir", which goes back to the time of Mahomet, what were called "Kefir grains" were added to produce the fermentation. These "Kefir grains" are now known to be little packets of "lactic acid bacteria" and yeasts.

In the case of bread-making there is a fermentation of the sugar in the flour, and this produces carbon dioxide, which makes the bread pleasantly spongy, very different from the compact "unleavened bread". In old days what was introduced into the dough was a little "leaven", that is to say, some dough reserved from a previous baking and containing numerous yeast-plants and other minute organisms. Later on this was improved on by the introduction of better and purer yeast bought from the brewer. Later still there came the use of carefully selected yeast-plants in the form of powder. But however the yeast be introduced it behaves in the same way, bringing about a fermentation of the sugar into alcohol with carbonic acid gas as a by-product. This makes the bread "rise".

But we must now inquire more minutely into the living agents that bring about certain kinds of fermentation. Towards the end

of the seventeenth century, the Dutchman Leeuwenhoek, who had an extraordinary talent for minute observation, saw the two chief kinds of fermenting organisms, namely, yeast-plants and bacteria. But he did not realise the importance of what he saw. It was not till about 1835 that the French physicist Cagniard de Latour recognised that the yeast used in brewing was composed of living cells that multiplied very rapidly by budding. He suggested in a somewhat vague way that they probably acted on sugar "through some effect of their vegetation".

A firmer step was taken about twenty years later when Pasteur proved beyond all possibility of doubt that alcoholic fermentation was due to the activity of the yeast-plant, and that the lactic fermentation of milk was similarly due to a "lactic acid bacterium". This was an epoch-making step.

The solid food that animals eat is digested in the food-canal, becoming fluid and more readily diffusible—and this process of digestion is in the main of the nature of a fermentation. But for many years a distinction was drawn between the non-living ferments in the digestive juices, like the pepsin of the stomach, and the ferments which are living organisms themselves, like yeast-plants and some bacteria. Rennet, which one buys in a shop when one wishes to make curds, is a preparation of the lining of the calf's stomach. When it is put into milk it coagulates the cheesy material, and we call the coagulation "curd". This rennet is almost, if not quite, the same as pepsin, the common ferment made by the gland-cells lining the stomach of backboned animals. No one regards rennet or pepsin as in any way alive, as the yeast is; and thus a firm line was drawn between the non-living and the living ferments, "organised" and "unorganised" as they were called.

But in 1897 Büchner subjected yeast to great pressure and heavy crushing, and extracted a yellowish juice which showed considerable power of fermenting sugar. This extracted yeast-ferment, which is called zymase, cannot be obtained quite pure; it is accompanied by another ferment which rather blunts its potency. But the point is that a non-living juice can act in the same way as living yeast-plants do when they change sugar into alcohol. They are able to do so, not because they are alive, but because they contain a ferment. Thus a somewhat artificial distinction was broken down.

Extracts of a few fermenting bacteria have also been prepared, and Büchner's important work was marked by the replacement of the word "ferment" by the word "enzyme", which is applicable to the fermenting chemical substance whether it works *inside* living cells, as in the case of yeasts, or *outside* living cells as in the digestive juices. It should be clearly understood that ferments are common in plants as well as in animals; thus a diastase ferment in every green leaf changes starch into sugar every evening, and a ferment

comparable to pepsin dissolves the hard protein stores in sprouting seeds.

The chemical nature of enzymes or ferments is not yet known. They are definite organic substances, but they do not seem to belong to any of the great groups—namely, the proteins (like white of egg), the carbohydrates (like starch), or the fats. It is not difficult to obtain concentrated essence of digestive glands like the sweetbread or pancreas, but the extract in such cases is a complex mixture, including for the gland mentioned at least three different ferments. Heat and powerful chemical reagents destroy these, and, though some progress has been made, no ferment has yet been isolated in a pure state, though there are rumours of a crystalline urease from certain plants. According to Willstätter an enzyme probably consists of two parts. One of these may be a protein or a carbohydrate in a colloidal state, but it serves mainly as the carrier of a simpler, chemically active substance of unknown nature, which is the ferment in the strict sense, though it cannot do its work without its carrier. Some of the properties of ferments depend on the carrier, but the particular power depends on the mysterious "active substance". And here it should be noted that the power *is* very particular, or as is said *specific*; thus an enzyme, which will cause the rapid fermentation of one kind of sugar, may exert no influence at all on another sugar closely related.

Most of the ferments are soluble in water or salt solutions and in glycerine. Each has a temperature at which it works best, and a particular medium that suits it better than any other.

But in what way are ferments peculiar? They quicken chemical changes, often prodigiously, yet they do not enter into combination with the substance that is formed as the outcome of the fermentation; a small amount, given sufficient time, is as effective as a large amount ("a little leaven leaveneth the whole lump"); a very minute quantity will often serve: thus a spoonful of rennet will clot 400,000 times its own weight of the cheese-forming substance in milk. When a substance acts as a quickener of chemical changes without being used up in so doing, it is called a *catalyst*, and all ferments seem to act as catalysts. But there are many substances, such as spongy platinum, which act as catalysts, though one would not call them ferments or enzymes. All enzymes act as catalysts, but all catalysts are not enzymes.

Another peculiarity of ferments is that in most cases their actions are "reversible". This requires some explanation. In many a mixture when a ferment is splitting up a substance—untying a knot of molecules—there is another change in progress working in the opposite way, tying the knot once more. At a certain point the splitting-up and the building-up attain the same velocity and no further change occurs, a condition of balance or equilibrium having

been attained. In fermentations carried on for practical purposes the product is gradually removed as it is formed, else what has been effected would often be undone. If the products of a fermentative action are removed as they are formed, and new fermentable material is provided, the enzyme goes on without being used up or enfeebled. This is often called the inexhaustibility of enzymes.

We referred in passing to spongy platinum, which has curious properties. If the metal in this state soaks up a mixture of oxygen and hydrogen at ordinary temperature, the two gases are brought very closely together. There is an enormous internal surface in the interstices of the metal, and on that surface the two gases are condensed and union takes place. So far as is known, nothing happens to the platinum, but it acts as a catalyst; and something like this happens with ferments. It may be that the colloidal nature of the ferment (with innumerable ultra-microscopic particles in suspension in a fluid) supplies a suitable surface on which a reaction takes place. But it is also possible that the ferment enters into *temporary* union with the substance that is being changed, and then gets free again to combine with more. As yet we do not know. But this is certain, that the vital changes that go on in our body and within plants and animals depend in great part on ferments, which are able to act very rapidly within small compass, which are able to do a great deal, though present in minimal quantity, which can go on and on without being exhausted by the changes that they accelerate. It has often been a source of wonder that living creatures can act and react so rapidly; part of the answer is to be found in the abundance of different kinds of ferments.

Let us take a glimpse at their great variety. There are those, like the pepsin of the stomach, which break down the large protein molecules that form an important part of our food. Others, like the ptyalin made by the salivary glands of the mouth, change starch into sugar. The sweetbread or pancreas forms a ferment that digests proteins, another that digests starchy food, and a third that changes fat into fatty acids and glycerine. There are ferments that work by taking up water, and there are others that split up water and liberate oxygen. Some enzymes break complex substances down, but others build up. It is not too much to say that life, whether in animal or plant, is quite inconceivable without ferments or enzymes.

They are all-important, but the difficulty is to understand how they work. Sir William Bayliss made a comparison which may help a little in regard to catalysts in general. Suppose a brass weight at the top of an inclined plane of polished plate-glass. If the glass is tilted at the right angle the weight slides down. But if the bottom of the weight is well oiled, the sliding down will be much more rapid. The action of a catalyst is like the action of the oil. In both cases there is a removal of some resistance to change—the friction

of the glass plate almost disappearing before the oil, the chemical coherence or inertia yielding before the catalyst or the ferment. And just as some oils work better than others, so it is with enzymes.

STRUCTURE AND LIFE OF THE CELL

THE CELL THEORY.—As we have seen, not a few of the early microscopists made attempts to define the minute elementary parts that build up living creatures; but it was not till 1838 that the idea of the cell as a structural and functional unit was clearly focused in the Cell Theory, or, better, Cell Doctrine (Zellenlehre) of Schwann and Schleiden. This generalisation includes three propositions. First, there is the *morphological* statement, that all living creatures have a cellular structure, and that all but the simplest, that is to

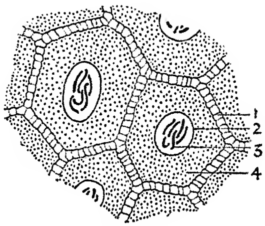


FIG. 47.

Two animal cells showing protoplasmic intercellular bridges between them After Pfitzner. 1, cell boundary; 2, nuclear boundary; 3, nucleoplasm; 4, cytoplasm.

say, all that have what may be called a "body", are built up of cells and modifications of cells. Even a minute "Wheel animalcule" or Rotifer, that can swim through the eye of a needle under the microscope, has nearly a thousand cells. The insertion of "modifications of cells" is to cover cases like a vessel in a plant, which may arise from the fusion of a row of cells, or like a long muscle-fibre in an animal which sometimes consists of several cells intimately united, or again, like the "syncytium" of some embroys (e.g. species of Paripatus), where the boundaries between adjacent cells are not well-defined. Second, there is the *physiological* statement, that the activity of a many-celled organism is the sum of the activities of the component cells. This idea requires to be safeguarded by the fact of correlation, for the life of the whole cannot be described without recognising that it is more than the life of all its parts, just as the behaviour of a crowd with a common purpose cannot be adequately described merely in terms of the movements of all the individuals. This correlation, elsewhere discussed, is more marked in the animal than in the plant, and most marked

in those animals that have well-developed nervous and vascular systems, and circulating chemical messengers or "hormones" which contribute greatly to the harmonious regulation of the whole life. Third, there is the *embryological* statement, that the individual many-celled organism begins its life, in all ordinary cases, as a fertilised egg-cell, which divides and re-divides to form an embryo. In other words, developing and growing imply cell-division. Here again there is some need of a saving clause, since it is not enough to picture the body being built up by adding cell to cell, as a house by adding brick to brick. There is an important idea in De Bary's caution: "It is not that the cells make the plant; it is the plant that makes the cells." For the cellular structure is an arrangement

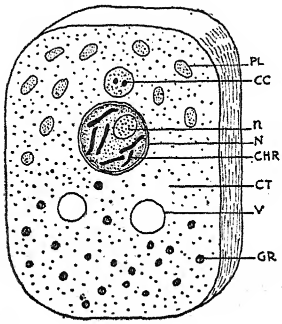


Fig. 48.

Diagram of a Typical Cell. PL, plastid; CC, centrosome; n, nucleolus; N, nucleus; CHR, chromosome; CT, cytoplasm; V, vacuole; GR, granule.

which makes it possible to have a body with much division of labour. Cellular structure is a condition of differentiation.

But after the formulation of the Cell Doctrine, it gradually became evident that the structure of the unit was complex to an unforeseen and extraordinary degree, just as the atom has slowly revealed the complexity of its organisation in modern physics. The main conclusions of Schwann and Schleiden remain true to-day, but the picture of the cell has become much more intricate.

Protoplasm and its Study.—In the early days of the Cell Doctrine more attention was paid to the cells than to their contents. The chemical aspect of life was but slowly appreciated, and what is obvious to every student to-day was not realised in 1840, that vital activity is essentially bound up with chemical and physical changes in the viscid matter that is present in almost all cells. It was largely through the study of unicellular organisms, like Amœbæ and Foraminifera, that the idea became clear that the kind of activity we call "life" was the outcome of changes in the contents of the cells.

The definition of this idea was largely due to Max Schultze in 1861, who was led from his studies of Protozoa to recognise that throughout all organisms the fundamental common basis is the viscid fluid which Dujardin had called "sarcode" and von Mohl, following Purkinje, had called "protoplasm". It was von Mohl's name that survived to denote what Huxley conveniently described as "the physical basis of life".

By protoplasm is meant the complex material that is essentially concerned with vital processes, and it is generally regarded as a mixture of substances which owe no small part of their virtue to their inter-relations with one another. It must be understood, however, that there may be many materials in a cell that are not to be included as part of the "living matter" or protoplasm. Thus there may be pigment granules, starch grains, crystals, globules of oil, vacuoles of water, and so on, which are not within the charmed circle of protoplasm. If the whole cell-substance be called *cytoplasm* and the relatively unessential granules and vacuoles, often of known chemical composition, be called *metaplasm,* then a good working definition of protoplasm would be "cytoplasm minus metaplasm". Examples of *relatively* pure protoplasm may be found in many minute egg-cells without yolk, as in sea-urchins, in blood corpuscles, in pollen grains, and in such simple organisms as Flowers-of-tan (Myxomycetes) and Amœbæ.

The student is familiar with the appearance of cells in sections that have been prepared for the microscope, and readers working by themselves should either make or purchase some typical preparations to show the structure of the cell. We give a short list of convenient objects for examination.

The egg-cells of star-fishes and sea-urchins.
The blood of the frog.
Section through the ovary of a mouse.
The green threads of Spirogyra from the ditch.
The hairs of the stamens of Tradescantia.
The epidermis stripped off a leaf.

The study of fresh material is often very disappointing, since at first one sees so little; and thus recourse is had to methods of fixing, staining, and clearing which bring out fine details of structure in the cell. The fresh specimen is first treated with a "fixative", such as osmic acid, corrosive sublimate, or formaldehyde solution—agents which have the property of causing what was originally a sticky fluid to "set" into a more or less firm jelly. The next step is cutting, either with a razor or a microtome, and this usually succeeds best when the object has been steeped in liquid paraffin, celloidin, or some other penetrating material that soaks in and fills up all the minute interstices, afterwards solidifying when cooled.

When the thin sections are made, the paraffin or other material is dissolved away, and some dye is used which will stain various parts of the cell differently. In many cases two or three stains may be used in succession to differentiate part from part more precisely. Finally, the section is (*a*) thoroughly dehydrated in absolute alcohol, (*b*) "cleared" of its fixative by soaking in benzol, clove-oil, or the like, and (*c*) mounted in a suitable preserving medium, such as Canada balsam. We have outlined this question of technique partly that it may be quite clear what has been done to the cells which have yielded the picture of detailed intricacy shown in book-figures, and partly for another reason of even greater importance. There can be no doubt that the methods of fixing and staining technique, of which we have given only a glimpse, have greatly contributed to the intimate modern knowledge of the microcosm of the cell. Without differential staining we could have known little of the complicated processes of cell-division and fertilisation, and a considerable part of the modern theory of heredity depends on the same possibility (see "Chromosome Theory of Heredity"). At the same time it has to be admitted that the technical methods by their very perfection led to an erroneous conception of protoplasm. A well-fixed and well-stained cell often shows an intricate visible cytoplasmic structure, which has been described as reticular, fibrillar, alveolar, and so forth. But it now appears that this visible microscopic structure is the result of the artificial treatment the cell has received. It can be induced, as Hardy showed, in perfectly structureless fluid gelatine or albumin. Moreover, the same cell will show different kinds of cytoplasmic structure according as it is treated. Apart from granules and plastids there is no visible *structure* in living protoplasm, though there is reason to believe in the presence of ultra-microscopic intracellular films which divide the cytoplasm into areas. These delicate films are occasionally to be seen around vacuoles in a cell.

Living protoplasm is a more or less viscous fluid in which innumerable ultra-microscopic granules and immiscible droplets are suspended. In other words, living protoplasm is in a colloid state. What are the evidences of this? The protean changes of form in an Amœba point to the absence of any permanent solid structure in the protoplasm, and so do the microdissection experiments which show that a needle can be drawn through living protoplasm without having any effect whatsoever. The absence of anything like a network is also proved by the simple observation that when there are drops of water within a living cell, these always assume a spherical shape. Another important fact is that minute granules in cells may sometimes be seen to be in constant "Brownian movement", which is due to their being continually buffeted by moving molecules of the fluid, in accordance with the kinetic theory of liquids. This is

best seen when the difficult method of "dark-ground illumination" is employed, in which particles too small to be seen even with the strongest lenses betray their presence by intercepting rays of light and appear as bright spots in a dark field. Further details are beyond our scope at present, but the interesting general fact is that the bright spots are seen to move freely through the protoplasm, which would not be possible if a solid reticulum were present.

The use of ultra-violet rays instead of visible light for microscopic photographs has also been helpful, for in this region of the spectrum of radiations some materials quite transparent to ordinary light appear opaque, and the detailed structure of cells is thus more easily discerned. Unfortunately, however, ultra-violet light has a disturbing action on fluid protoplasm.

In ordinary microscopic observation, whether with visible or with ultra-violet light, the object examined absorbs some of the transmitted light reflected through it from the mirror, and the structure of the object appears relatively opaque or coloured. In the "dark-ground" method, no light reaches the eye at all except in so far as rays are refracted or scattered by particles in the object itself. The illumination of the object is in a horizontal, not in a vertical direction.

No amount of mere magnification will make it possible to see definitely a particle with a diameter less than one five-thousandth part of a millimetre. It is too small for the light-rays of the wave-lengths visible to our eyes; "resolution" cannot be obtained with any system of lenses. No object smaller than half the wave-length of the light used can be seen with any definiteness. This is a matter of considerable practical importance in the study of the "filterable viruses" which are believed to contain organisms smaller than bacteria that are associated with such diseases as hydrophobia, measles, foot-and-mouth disease, and cancer.

But when the object is altogether below the limit of resolution by ordinary microscopy, it is still possible to detect its presence by an extension of the "dark-ground" method—the so-called "ultra-microscope", an instrument first used by Siedentopf and Zsigmondy in 1903. Everyone is familiar with the fact that dust particles, which are absolutely invisible in the ordinary daylight of a room, may be detected in thousands when a strong beam of light suddenly enters. In actual fact the invisible does not become visible, for what we see are the rays diffracted from the surface of the brilliantly illuminated particles. Similarly, the strong horizontal beam used in the ultra-microscope reveals shining points of diffracted light from minute particles in a fluid. The more intense the illumination, the greater the possibility of detecting minute particles, and this goes as far as the starch molecules in a solution! It must be emphasised, however, that the particle detected is only indirectly

visible; it is not seen, it merely betrays its presence by scattering light rays.

Another new method which has notably increased our knowledge of protoplasm is the "micro-dissection", which is especially associated with the names of Kite and Chambers. Some of the early naturalists, before microscopy began to be an everyday method, were masters in the art of minute dissection, unravelling the food-canal of a flea or separating out the intact brain of an ant, which Darwin called the most marvellous atom of matter in the world. With good eyes, steady hands, sharp needles, and no end of patience, it is possible to do very extraordinary things, but there are obvious limits to *direct* manipulation. It is on indirect manipulation that the new method of micro-dissection depends, and many of its successes are very striking. Prof. Robert Chambers of Cornell University is able to inject an Amœba, which is just visible to the naked eye as a white speck against the dark mud. It is often about a hundredth of an inch in diameter. From the centre of an egg-cell even smaller than this, Prof. Chambers is able to jerk out the nucleus, and he can divide the same cell into several pieces. This has been done before, but it may be noted that in *most* of the early experiments with separated-off pieces of egg-cell, those of Prof. Delage, for instance, the method used was not micro-dissection but shaking the egg-cells in the fluid in which they were floating.

How does Chambers effect his manipulative marvels? The object to be micro-dissected is included in a "hanging drop" suspended from the under-side of a cover-glass firmly fastened on the stage of the microscope in the field of vision. The cover-glass forms, as it were, the roof of a moist chamber that has no floor. Into this space there protrude the exquisitely fine tips, straight or curved or bent at right angles, of glass needles which are fixed in holders. These holders again are attached to an ingenious system of screws fastened on the under-side of the stage of the microscope. The object cannot be seen with the naked eye, but it is quite clear in the centre of the field of the low-power or high-power microscope, and so are the points of the needles. By working the screws it is possible to move the needles up or down, as well as in a horizontal plane, and it is not difficult to bring the very delicate tips together. Thus one tip may be used to press the cell against the firmly fixed cover-glass, while the other is used to cut a piece off. It is possible in this way to isolate a particular portion of a cell and to watch what happens. The method can also be used to good practical purpose in isolating a single micro-organism, so that an absolutely pure culture or "pure line" can be secured. It is probable that this method of micro-dissection has a great future before it.

Our present question, however, is: What does the method indicate in regard to the nature of protoplasm? All the evidence points to

the conclusion that active protoplasm is a fluid of very varying viscosity; that it is often crowded with mobile granules which, however, are unessential; that it is homogeneous except in so far as there may be transient films dividing the cell-substance into areas; and that it always forms a surface film and forms it afresh when it is destroyed.

In many cases the protoplasm changes from a fluid "sol" state to a jelly-like "gel" state. Up to a limit this is reversible, and there may even be an alternation between more solid and more liquid conditions in one part of the cell, notably in amœboid movement. Leaving further details for subsequent discussion, we may describe protoplasm as consisting of diversified organic material partly in colloidal and partly in true solution, and of a percentage of mineral salts, all dissolved in water, which forms about 80 per cent. of the total.

Let us sum up. While there is "one kind of flesh of men, another flesh of beasts, another of fishes, and another of birds", the term protoplasm indicates that in all kinds of "flesh" there is a more or less similar physical basis. The word was invented by Purkinje in 1840, but von Mohl seems to have been the first to use it as a general term for the kind of material that goes to the making of all living creatures. Writing in 1846, he said: "The remainder of the cell is more or less densely filled with an opaque, viscid fluid of a white colour, having granules intermingled with it, which fluid I call protoplasm." The modern student would be inclined to change some of von Mohl's words, saying clear instead of opaque, colourless instead of white, but in most ways von Mohl's description holds good still. Perhaps the two main advances are that we think of protoplasm as an intricate mixture of proteins, carbohydrates, fats, ferments, and mineral matter, and that we think of it as in a colloid state. The multitudinous particles of protein and other substances, and the crowds of unmiscible droplets as well, present a very large surface in proportion to the total mass. This allows of great intensity of chemical and physical changes, because the area of the surface is proportionally so enormous. Thus there is usually an electric charge on the contact surface between any two "phases", e.g. between a complex solid particle and a complex liquid medium. As the multitudinousness of the particles, often quivering under the bombardment of the restless molecules of the fluid, means a very large surface, there is consequently a copious spring of electrification. Many of the properties of living matter are wrapped up with this colloidal state.

Two difficulties, often stated by the thoughtful student, may be met at this point. If protoplasm is a liquid emulsion, mostly consisting of water, how are animals as firm as most of them are? and how do trees rise three hundred feet into the air? Part of the answer

is that a high degree of stability may be attained by turgidity, which practically means the intracellular pressure on the cell-walls. The stem of the common Mimulus is mostly water, but it serves to raise the golden flowers far out of the ditch. This is because of the turgidity of the cells; and the same is true of the cells composing the lips of the jelly-fish or the notochord of the lancelet.

The second half of the answer is that protoplasm continually tends to make for itself a supporting framework. In the simplest cases the living matter secretes a non-living material that serves as a sort of scaffolding for further growth. There is a precipitation of non-living waste materials; in a few cases by-products of everyday activity may be utilised; in other cases the protoplasm may die away; in one way or another protoplasm may make for itself a supporting framework.

The other difficulty concerns the division of labour within the cell, which may be usefully compared to a one-roomed house, with a multitude of activities all occurring at once within a limited radius. Why do they not interfere with one another? The modern answer to this question is simply that protoplasm is a film-pervaded or film-partitioned system. The living cell is partitioned with extremely delicate films, not usually demonstrable in any direct way, which have diffusion-hindering properties, and thus allow dissimilar chemical processes to occur in contiguity. So we have exchanged the visible intricacy apparent to earlier histologists, but very largely artefact, for an intricacy that is usually invisible, yet seems to be real.

THE NUCLEUS.—The microtechnical methods referred to in connection with protoplasm have also been utilised in the study of the nucleus, which was discovered by Robert Brown, whom Humboldt called "facile princeps botanicorum". Here, however, the picture presented by fixed and stained specimens seems to correspond a little more closely to reality. In a normal resting nucleus there is a fine skein of a material called "linin", and on this there lie scattered granules of a protein substance which stains deeply and is therefore called chromatin. The nucleus also contains a compact body called a nucleolus, or there may be more than one. In some cases a nucleolus seems to be a reserve of chromatin; in other cases it is more like a globule of waste material; in general, a nucleolus is an inconstant and variable portion of the nucleus. Bathing the chromatin there is a complex nuclear sap or karyolymph, and surrounding the whole there is a nuclear membrane—a "semi-permeable" membrane which lets certain substances, but not others, in and out, in the give and take between nucleoplasm and cytoplasm.

Such is the resting nucleus of a cell, but in the ordinary process of cell-division (the mode known as "karyokinesis" or "mitosis"), the

appearance becomes very different. The skein or network disappears, and the chromatin becomes concentrated into sharply defined bodies called chromosomes, definite in number for each species. Just outside the nucleus, and probably arising from it, is a small body called the centrosome. This divides into two, and the two halves move to opposite poles of the nucleus and become the centres of what appear in the fixed cytoplasm as very delicate rays. At the equator of the nucleus the chromosomes arrange themselves in a horizontal plane, at right angles to the long axis of the cell, or to the line between the two centrosomes. Each chromosome is then split up the middle longitudinally, as one might split a wooden

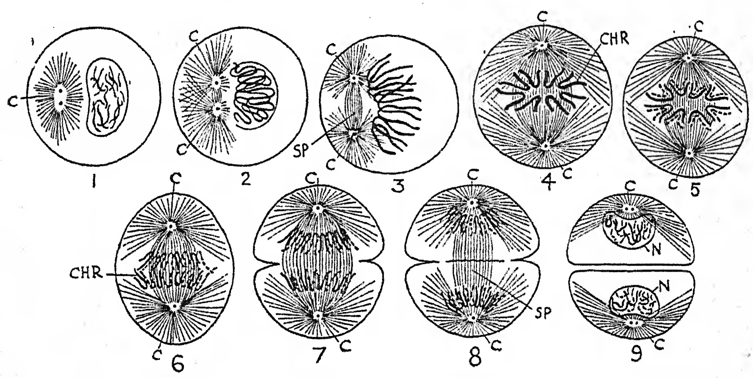


FIG. 49.

Diagram of Typical Cell-division. After Ziegler. 1, The resting nucleus, with centrosome (C); 2, the centrosome has divided into two; 3, the chromosomes are now well-defined; 4, chromosomes grouped at the equator; 5 and 6, each chromosome is longitudinally split; 7, the halves of the chromosomes retreat towards the poles; 8, a new cell membrane is formed; 9, the daughter cells are now quite distinct and the nuclei are passing back into the resting phase.

match into two. The limits between the nucleus and the cytoplasm outside become vague, and the round appearance of the nucleus is replaced by a more or less biconical spindle shape. Then a remarkable thing happens: one-half of each longitudinally split chromosome moves towards each centrosome—pushed or pulled, who shall say? In any case, the half chromosomes move along the delicate fibres which run from centrosome to centrosome (so forming the "central spindle") or from centrosome to equator (the "equatorial spindle"). In this arrangement there is a curious likeness to that of iron filings round a magnet or arranging themselves on a plate under electrical influence. Then the cell constricts and separates the two poles from one another, thus soon forming two daughter-cells, each with its normal number of chromosomes, and each with a centrosome. The chromosomes gradually sink back into the resting

network state, and there is a restoration of the apparently simple *status quo* after a complex and meticulously precise process of division.

A study of fixed and stained material gives us the succession of precise pictures which we have scantily outlined, but this is rather disturbed by the results of fresh examination under the microscope and with the micro-dissection apparatus. For the nucleus is seen to be clear and structureless. It resembles a membranous bag filled with fluid, though some kinds of nucleoli are more solid. Yet the nuclear fluid is extraordinarily apt to set into a firm jelly. and this is brought about by various stimuli, even including slight mechanical injury. In the resting nucleus the jelly may show the chromatin network structure; and, if it sets just before the division process begins, the threads of the net may seem more delicate than usual. During the process of division, when the membrane of the nucleus has disappeared, the nuclear spindle has a strong tendency to set or coagulate. One must remember that in the actively moving Amœba, giving off outflowing finger-like processes or pseudopodia, there is an alternation of "sol" and "gel" states. The nucleus has a strong tendency to pass into the "gel" state, when differentiations previously invisible may become patent. But the results of studies on living material all point to the conclusion that the living nucleus at rest is *a structureless fluid*, except for certain kinds of nucleoli.

What, then, is true of the chromosomes, believed to be the vehicles of the hereditary characters? In successfully fixed and stained cells, such as the egg-cells of the horse's maw-worm, they stand out with extraordinary clearness, substantial countable bodies, with precise shapes (spherical, rod-like, V-like, K-like, and so on). They are undoubtedly real and definite bodies, or perhaps one should say differentiations. If the homely comparison is permissible, they may be likened to as many minute and very unsubstantial sausages, which readily change from "sol" to "gel", and are each surrounded by a surface film. Besides the typical mitotic cell-division we must take account of other modes, notably amitotic and meiotic.

Cell-inclusions.—Our discussion of the structure of protoplasm expressly left out of count the various visible bodies included in the clear fluid; these cannot, however, be entirely neglected. There are usually granules in the cytoplasm, distinguishable as small *microsomes* and larger, somewhat unstable *macrosomes*. They refract light sharply and are therefore easily visible. They are heavy and can be separated from the protoplasm by means of the centrifuge; they often show streaming movements which indicate the fluid state of the protoplasm. The Echinoderm egg is a good example of a cell crowded with granules. Certain specialised cells may contain special inclusions; for example, those of the green plant and of a few Protozoa contain plastids, in which chlorophyll is concentrated, and

which are probably the seat of the photosynthetic process (*q.v.*). Moreover, the essential nuclear material (chromatin) may occur in the external cytoplasm, as granules called chromidia; indeed, some of the lowest forms of life have no definite nucleus. The Nissl bodies of nerve-cells are of the same type, but in some cases it is doubtful whether the definite granules visible are not formed by precipitation on the death of the protoplasm.

Constant but elusive constituents of cytoplasms are the mitochondria, which are destroyed by the more usual methods of fixation, and hardly visible in the living cell except with the dark-ground illumination; fortunately, they can be made visible by staining the *living* cell with a particular dye (Janus green B). They are rod-like or thread-like, semi-solid, constantly in motion, and their function remains quite obscure. Some have held that they are not truly part of the cell, but independent organisms—bacteria (Altmann, Portier, Wallin), a view which has little to commend it; while others have gone so far as to ascribe to the mitochondria an important part in the handing-on of the inheritance from one generation to the next, although the paramount importance of the chromosomes in this respect is now very widely recognised. They are probably foci of particular processes of metabolism.

Somewhat similar in its properties, but less readily demonstrable in living cells, is the "internal reticular apparatus" of Golgi. In vertebrates this appears as a dense network, often as large as the nucleus, and usually lying in a definite position in the cell; in invertebrates it is more scattered; it occurs in Protozoa and in plants. In gland cells the apparatus is always found between the nucleus and the lumen or passage into which the secretion of the cell is poured; while in Protozoa it may form a ring round the contractile vacuole, which is usually regarded as a means of getting rid of the waste-products of the cell's chemical activity. It seems very likely that the apparatus has something to do with the accumulation of materials, useful or useless, which are shortly to be discharged from the cell—secretion or excretion. But our knowledge of this, as of the mitochondria, chromidia, and other constituents of the cytoplasm is still all too incomplete.

TYPES OF CELLS.—Many of the Protozoa are so highly organised that it seems clear to speak of them as non-cellular rather than as single cells; but the Amœba at least is so simple that it may fairly be regarded as the most generalised type of cell, displaying within itself the five great functional properties, of contractility, irritability, secretion, growth, reproduction. That is, it has the powers of movement, of responding to stimulation, of forming new substances from the food materials with which it is supplied, either to add to its own size or for special purposes, and eventually of dividing

into daughter-cells. And along with these may be set the power to generate electric currents, a feature of the life of the cell whose significance is not yet fully appreciated. These properties can only

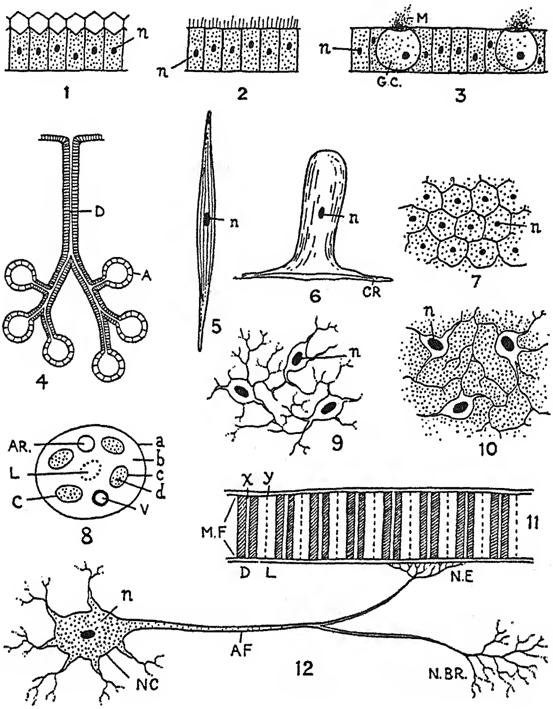


FIG. 50

Diagram of Various Types of Animal Cells. 1, Columnar epithelium: *n*, nucleus throughout; 2, ciliated epithelium; 3, glandular epithelium, with goblet cells (GC) making mucus (M); 4, a compound branched gland, A a cluster of gland-cells (alveolus), D the efferent duct; 5, smooth muscle-cell; 6, an ectoderm cell of Hydra, with contractile roots (CR); 7, surface view of squamous epithelium; 8, diagrammatic section through a nerve; C, a bundle of nerve-fibres; AR, an artery; V, a vein; L, a lymph vessel; *a*, external sheath or epineurium; *b*, supporting matrix of the nerve; *c*, perineurium around a bundle of nerve-fibres (*d*); 9 and 10, networks of connective-tissue cells, without and with a matrix; 11, a striped muscle-fibre (MF) with alternate dark (D) and light (L) bands; *x*, a median line across a dark stripe; *y*, the same across a light stripe; 12, a motor nerve-cell or neuron (NC), giving off short dendrites and a long axon (AF) which gives off a ramifying branch (NBR) and another (NE) nerve-ending on a muscle-fibre.

be maintained if there is within the cell a constant supply of energy derived from chemical reactions. This supply of energy normally implies *nutrition*, the supply of food materials; *respiration*, the supply

of oxygen to combine with at least a part of the food materials; and *excretion*, the discharge of the products of the reactions. Thus there are six great properties maintained by three great processes; and in the Amœba there is a balance between them. There is an absence of over-emphasis on any one phase to the exclusion of the rest; and this means that the one-celled individual is physiologically complete in itself to a degree that cannot be said of most of the cells composing a multicellular organism.

Casually examined, the Amœba is a blob of viscid protoplasm of irregular and changing shape, containing numerous dark granules, clear spaces or vacuoles, and a central body of more definite shape and solid appearance, the nucleus. Very similar in appearance are the leucocytes or white blood cells of the Vertebrates; indeed, these are hardly less independent or less complete in themselves than the Amœba. But specialisation is the dominant note in the cells of the Metazoa (just as specialisation for particular conditions of life is seen in the more highly organised Protozoa), and these specialisations of cells deserve to be noticed.

In the blood of mammals the Amœba-like white cells are far outnumbered by the red blood corpuscles, small disc-like cells whose chief function—that of carrying oxygen combined with the pigment with which they are highly charged—quite dominates over the other activities of the cell, so that there is not even a nucleus. There may be five million of these cells in a cubic millimetre of blood. Less specialised are the cells of epithelial tissues, which are found as coverings in the body, in part externally, but also lining the alimentary canal, the air passages, the blood-vessels, and so on. Their chief adaptation is that of presenting at the surface a compact pavement, which may, in certain cases, be ciliated. Or again, the cells may be glandular, with the power of forming special substances (such as digestive juices), which they pour out into the cavity they surround. Much more specialised are the nerve-cells. These have a central portion of very variable size and shape surrounding the large nucleus, and a series of fine processes, often also several short branching connections to neighbouring cells, and finally a single nerve-fibre of very great length, along which the efferent or outgoing nervous impulse travels. Then there are the cells of smooth or unstriped muscle, which are elongated spindles, an oval central part with the nucleus and extending from this in opposite directions the fibre-like portions with the power of contraction. Striped or skeletal muscle, again, is still more highly specialised; the fibres may be over an inch long and angular in section; close to the surface may be seen the nuclei, of which there may be even many hundreds in a single fibre, though each fibre behaves as a single cell. In the connective tissues, which include bone, cartilage, and fat, there is usually a light scaffolding of

straggling cells and a non-living ground substance of very variable nature, according to the particular kind of tissue. This brief survey of cell-forms may fittingly conclude by contrasting the mobile male germ-cell or spermatozoon, with its small head composed almost wholly of nuclear material, and its vibratile tail, with the large, round, sluggish female germ-cell, whose characteristic response to such a stimulus as the entry of the spermatozoon—that of dividing and growing and redividing until the complexity of the parent body is reproduced—is the most marvellous of all the faculties of cells, and one, of course, entirely lacking in such a generalised type of cell as the leucocyte.

IRRITABILITY.—All living cells have the property of being irritable or reactive, of changing within themselves in response to changes in their environment. In the case of many irritable tissues, the stimulus of an increase in the sodium content of the medium causes a reaction or response, namely, an increase of permeability of the cell-wall, while the response to increased calcium content is just the opposite. Cells are sensitive to other changes in the environment besides purely chemical ones; for example, the cells of the organs of smell and taste are sensitive to chemicals, but the cells of the retina to changes in illumination, and various nerve-endings in the skin to changes of temperature or to pressure. In all cases the important response is that a message is sent along a nerve-fibre towards the brain. Single-celled organisms are also sensitive to light, heat, chemicals, contact, or electrical currents, and may react by various changes in their behaviour. Or again, gland-cells secrete or muscle-cells contract in response to a stimulus, which may be a nerve-impulse or an electrical or chemical change.

The case of muscle-fibres may be examined rather more closely. A change in the relative concentration of the salts of the medium may produce a contraction, but in certain conditions (anaphylaxis) this response is evoked by the appearance of a particular protein and by no other—a remarkably delicate *selective* reaction. In the case of electric stimulation, an important fact stands out: the muscle is not affected by the continuous flow of a current, but does respond to any change, whether increase or decrease, if it is sufficiently great and sufficiently sudden. Moreover, the reaction is always the same, both in type and in quantity: for striped muscle-fibres, nerve-fibres, and various other kinds of irritable cells, obey the "all-or-none" rule; there is complete contraction or there is none; a nervous impulse is sent at constant strength if it is sent at all, and so in the other cases. Finally, it should be noted that after response there is a *refractory period*, during which the irritable cell is not sensitive to stimulus, although in the case of nerves this may be exceedingly short: there is some process of reloading, or rebuilding of a structure

affected by the initial stimulus and its response, before a further reaction can be obtained.

It is quite conceivable that the word "structure" in the last sentence is to be interpreted in a definite physical sense, as a series of surfaces of the kind we described in the section on permeability, forming some sort of structure within the cell. There is very clear evidence that in many cases, at least, the first response to stimulus is a change in permeability, sometimes of the external film, sometimes, perhaps, of internal partitions. The best case is that of the sensitive Mimosa, where the erect position of the leaves and petioles depends on the cells being maintained in a state of turgor or distension by water, which in turn is due to the semi-permeable nature of the membrane and the osmotic pressure produced in this way. When the plant is touched, the membranes lose their power to prevent dissolved salts from passing, and the solution escapes from the cell; as a result, the tissue loses its rigidity and the cells collapse, so that the leaves move. The same thing is seen in the Venus' fly-trap. In the animal kingdom it is harder to demonstrate this directly, but in the case of the ovum, which responds to the stimulus of the entering spermatozoon (or to certain artificial treatments) by beginning to divide, a considerable increase in permeability is demonstrable.

The next point to be considered concerns the electric currents produced by the cell, of which we have said little since they were first mentioned in the introductory section on the cell. The first evidence of response in any irritable tissue is an electric one. In the case of a muscle-fibre, there is a sudden electrical change, which may be completed in the "latent period" before the actual contraction begins. Now it has become plain that there is a very close connection between these electrical changes and alterations in permeability. If there can exist a membrane which is permeable to one of the ions of a salt and not to the other, then there will be a difference of electric potential between the two sides of the membrane; any condition which alters the permeability of the membrane with respect to the ions will cause a change in this potential difference, which in turn will produce an electric current. These membrane theories of the electric properties of the cell have been worked out for plant cells by Loeb and Beutner; it is shown that mechanical injury of the cell-structure causes an "injury current" due to the local disturbance of the potential difference normally existing on the two sides of the membrane.

These electrical currents are probably of the greatest importance in the *conduction* part of the response to stimulus. When the spermatozoon enters the egg, a wave of change sweeps all round the surface from the point of entry. Again, if part of a muscle is rendered incapable of contracting by soaking it till it becomes water-logged,

it may still be able to transmit the impulse to an unaltered portion of the tissue, which contracts; this shows that conduction and the typical response (contraction) are not inseparable. The importance of the electric currents is that they are able to pass from one cell to another. For example, even the spermatozoa in a group with no organic connection between them are found to influence each other's movements, so that they are soon all vibrating in unison; it is hard to explain this except by an electrical transmission.

We must not omit a note on the subject of cell-rhythm. Many cells display a tendency to rhythmicity in their activities, for example, in the beating of cilia. Again, the cells of the heart-muscle in Vertebrates have a tendency to contract rhythmically quite apart from nervous stimulation, which they show even when isolated from the organ and grown in "tissue cultures". In other cases the rhythm originates in the nervous system, which sends out periodic impulses. W. J. Crozier has recently studied a number of cases of this sort, such as the rhythmic flashing of fire-flies, the chirping of crickets and the beating of the heart of Arthropods: in all these cases temperature has an effect on the frequency: and (by the use of the "Arrhenius-equation" for the effect of temperature on the velocity of reactions) Crozier has shown that it is likely that in all these cases the motor impulses from the nervous system, which determine the activities of the organs controlled, *are the same,* whatever their nature may be.

In concluding this survey of the structure and activities of the cell, we may well return to an insistence on the idea of films of protoplasm forming surfaces, certainly at the exterior, and perhaps also within the cell. We have seen that the network produced by the histologist's fixation of cells is an artificial structure; and also that dyes and salts diffuse freely through the protoplasm; so that the idea of a network of partitions dividing liquid protoplasm into a honeycomb is very improbable. On the other hand, there is no doubt as to the importance of surface for chemical reactions, more especially for those catalysed by enzymes. Furthermore, Warburg has pointed out that the surface of porous charcoal may serve as a model; since various substances, otherwise resistant, are oxidised thereon, always provided that iron is present to act as a catalyst, *as it does* in the living cell. The lowering of the chemical activity of the living matter which follows upon mechanical injury has been mentioned; and in this section the connection between permeability of membranes, irritability and especially electrical response, has been hinted at. Narcotics, which depress the chemical activity of the cell and lower its reactivity, are typically "surface-active" compounds, soluble in fat-solvents. Moreover, it is known that after death, when the permeability of the membranes is increased, enzymes previously locked up in some way attack and destroy the constituents

of the protoplasm (autolysis). From all this, it will be seen that in spite of the difficulties, in spite of our ignorance of the nature of even artificial semi-permeable membranes, and the very much greater complexity of behaviour of the protoplasmic films, the idea of some kind of physical structure within the cytoplasm is not easily discarded. It is possible that such structure may be diagrammatically represented by a large number of minute and more or less separate plasmic spheroids, each of which is a "film", with the chemical, electrical, and permeability properties outlined in preceding sections (and possibly with the structure suggested by Clowes); each may surround a mitochondrion or other "inclusion"; and all are floating or flowing in a continuous medium of more homogeneous and more viscous protoplasm; while the whole is bounded by the more substantial plasmic membrane of the surface of the cell.

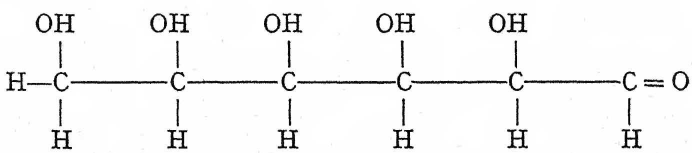
Cell Materials.—The main chemical elements present in living matter are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, and iron; but many more may be present, often in mere traces, including such unlikely things as arsenic, fluorine, and zinc. The *important* fact is that very common elements are formed into the physical basis of life; the *curious* fact is that rare elements sometimes occur in small quantities. In illustration of these rarities argon may be mentioned, the gas that Lord Rayleigh and Sir William Ramsay discovered about the beginning of this century in the atmosphere. In a paper published in the *Comptes Rendus* for August 1925, it is reported by Pictet, Scherrer, and Helfer that argon is present in many kinds of living cells. The investigators found it in active yeast-cells, in the fresh cells of a sheep's brain, and in the newly drawn blood of a bullock. They seem to have satisfied themselves that the argon is present in the cells as an integral part of their substance, and not simply hanging on by superficial adsorption. Yet till compounds of argon are known, the probability remains that it occurs as an included gas in the living cells.

But the catalogue of elements found in living matter helps very little towards an understanding of the chemistry, for that depends essentially on the complex organic molecules. Of these the most important are the proteins, which are regarded as the most essential and the most specialised of the identifiable constituents of protoplasm. The molecular weight may be 33,000, or several times this; and though formulæ may be given indicating percentage composition, such as $C_{55}H_7N_{18}O_{24}S_2$, the construction of these giant molecules remains unravelled. It is known, however, that they consist mainly of large numbers of molecules of amino-acids, all linked together.

The amino-acids, of which there are about twenty common kinds, form a very heterogeneous group of substances. They all contain

carbon, hydrogen, oxygen, and nitrogen, and some (e.g. cystein) also contain sulphur. They range from simple straight-chain forms, such as glycine (amino-acetic acid) $NH_2 . CH_2 . COOH$, to forms containing the benzene ring such as tyrosine or even more complex rings, as in the case of tryptophane. The particular amino-acid called tyrosine, from the Greek word for cheese, was obtained by Liebig by heating up cheese with potash, and the fundamental fact that proteins are built up of interlinked amino-acids may be re-emphasised by noting that tyrosin is the most readily isolated of the amino-acids into which casein, the chief protein of cheese, breaks up. As amino acids play a very important part in the life of the body, we must dwell on them for a moment longer, while referring the student for details to the luminous *Fundamentals of Bio-Chemistry* by T. R. Parsons (Cambridge, 1923). Amino-acids have great capacity for uniting with other substances, and they all act not only as acids, but as bases by virtue of the nitrogen-containing part of the molecule. This *power of uniting* is characteristic of proteins also, and they too can form salts with either acids or alkalies. Indeed, it is only at a point in the region of neutrality that they exist by themselves. Moreover, quite apart from the salts they form, proteins have a great power of combining with other organic substances, such as sugars and pigments. For the biological student, the important fact is that the proteins and their amino-acids, the two kinds of substances pre-eminently characteristic of protoplasm, have extraordinary powers of entering into combinations.

The second class of materials includes the carbohydrates, such as the sugars, and they present fewer difficulties. The simpler sugars are chains of five or six carbon atoms united with hydrogen and oxygen, thus glucose or grape sugar ($C_6H_{12}O_6$) may be represented as



But there are higher sugars (disaccharides), like cane sugar, malt sugar, and milk sugar, whose molecules contain twelve carbon atoms instead of five or six. In still more complex carbohydrates, such as starch and glycogen, which form very important stores in plant and animal cells respectively, the structure is so complex that it has not yet been exactly determined, and it may be useful to linger over the fact. The empirical formula of starch is $C_6H_{10}O_5$, indicating the proportions in which the elements carbon, hydrogen, and oxygen occur, but this does not inform us as to the structure of the starch molecule. When it is attacked by

the ordinary weapons of chemistry, such as strong acids and caustic alkalies, the large molecule of starch breaks down into several very much smaller molecules of comparatively simple sugars. Recently, moreover, chemists have begun to suspect that "starch" is really a mixture of two or more chemical compounds. Each grain of starch possesses a tough outer envelope of "amylo-pectin", which will not dissolve in water, and a less resistant core of "amylose" or "granulose". But there is an additional and unsuspected complication. The recent work of Ling and Nanji shows that the outer envelope of amylo-pectin contains a considerable proportion of the element phosphorus. Now phosphorus is an important constituent of all living cells, and it is likely that this hitherto undetected store of phosphorus in the starch grains is of great importance to the plant, and perhaps also to the animals that reincarnate what the plant has made. This instance illustrates what happens so often in the advance of science: an apparently simple thing (the composition of starch) turns out to be more complicated than was supposed, and the unravelling throws light on something fundamental (in this case the phosphorus cycle).

Before passing from the carbohydrates, it should be noted that the complex forms resemble proteins in forming *colloidal* solutions in water, their large molecules cohering in particles, while the simple sugars resemble the amino-acids in forming *true* solutions, in which the molecules float free.

The third group of cell materials includes primarily the fats, in which glycerol (popularly called glycerine) combines with three molecules of fatty acids. The glycerol molecule contains three $-OH$ or hydroxyl groups

$$\begin{array}{l} CH_2.OH \\ | \\ CH\ .OH \\ | \\ CH_2.OH \end{array}$$

and each of these unites with one of three acids, stearic, palmitic, or oleic, to form three common fats, which usually occur together in ordinary animals. The fatty acids have long, straight chains of carbon atoms; thus stearic and oleic have eighteen, palmitic sixteen. When they combine with a mineral base, such as caustic soda, they form soap. Perhaps this slightly technical paragraph, familiar enough to the student of chemistry, may be more intelligible to others if the familiar fact be kept in mind that ordinary soap consists of the sodium salts of stearic and palmitic acids, that it is made by boiling up fats with caustic soda, and that glycerine is always produced at soapworks. In other words, fats consist of glycerol united to fatty acids.

Along with the fats are classed the lipoids or fat-like substances, of which the most important is lecithin, which occurs, along with the protein vitellin, in the yolk of many different kinds of eggs. Its formula begins like that of the fats, but ends quite differently with an atom of phosphorus and a nitrogen-containing base. There are other members of this class which become wrapped up with sugars. Of the importance of these and other substances in the chemical routine (or metabolism) of the body, account will be taken in the section on "Everyday Functions"; we are here concerned simply with a survey of cell materials.

So far, then, in this stocktaking of cell materials, we have recognised:—

(1) the proteins and their component amino-acids; and the compounds that proteins form, especially with nucleic acid;
(2) the carbohydrates, such as sugars and starch;
(3) the fats, with their associated lipoids, and
(4) mineral salts, iron, and so forth.

Along with these organic compounds and abundant water (80 per cent.), there are always to be found mineral salts, such as potassium chloride. And there are also traces of other elements, especially iron, which have to be fitted in eventually into the cellular framework. But here, if our simple general perspective is to be maintained, must end our survey of the chemical materials of the cell.

STAINING.—It may now be asked with reason whether anything is known of the combination of dyes with the constituents of the cell in fixed and stained microscopical preparations. It must be frankly admitted that the answer is disappointing; we know too little of the nature of these combinations, and our ideas of the location of various substances within the cell is very vague. The dyes generally employed in microscopy fall into two great classes, acid dyes and basic dyes. But it must be realised that in fact most of the dyes are neutral salts, and the term "acid dye" means a dye with an organic acid and a mineral base. The basic dyes, which have the opposite chemical structure, are divided into those which (like methylene blue and gentian violet) stain the fixed tissues directly, and those (like hæmatoxylin) which may require a mordant solution to prepare the way before them; they combine with the nucleus, especially with the nucleolus or the chromosomes—in fact, with chromatin. On various grounds the conclusion is arrived at that chromatin or nucleo-protein is a salt of basic protein and nucleic acid; this acid it is which combines with the basic dye, and its chemical nature, although complex, is so far known; it appears to contain phosphoric acid, sugars, and nitrogenous bases; there seems to be one sort of nucleic acid for

plants and another for animals, while the protein with which it is combined is different in every species of organism.

The acid dyes—eosin, orange G, picric acid, and so on—combine with the fixed cytoplasm, while others of the group (methyl blue, acid fuchsin) have a special affinity for cytoplasm which has become toughened in the specialisation of connective cells. In some cases fixation is as informative as staining, not that this is saying very much. Thus osmic acid blackens and alcohol dissolves fat-like substances. On this is based the conclusion that both mitochondria and the Golgi apparatus consist of compounds of lipoids with proteins.

CHEMICAL PROCESSES WITHIN THE CELL

In the previous section account has been taken of the chemical *materials*—the proteins, carbohydrates, fats, and so on, which are present in the cell; the question now rises: What chemical changes are of common occurrence? All cells are laboratories in which chemical reactions supply energy, which may do work as in muscular activity, or may produce "animal heat", or may facilitate some other associated chemical reaction. In nearly all cells the energy-yielding reactions are of the nature of *combustions or oxidations*, as Lavoisier first made clear when he emphasised the analogy between the life of an animal and the burning of a candle. When organic carbon compounds are burned, most of the carbon combines with oxygen, and carbon dioxide results; most of the hydrogen combines with oxygen, and water results; but nitrogen, if it is present, as in proteins, is not easily oxidised; it sometimes takes the form of ammonia, as in the burning of feathers. Similar changes go on in the living cell.

An organic molecule is said to be oxidised when oxygen is added to it, even if the process does not go so far as its complete "burning away". If oxygen is taken from the organic molecule, it is said to be reduced. In these processes there is an evident antithesis between oxygen and hydrogen, for if hydrogen is added to a molecule, it will require more oxygen for complete combustion, while if hydrogen is taken away less oxygen will be required. Therefore the removal of hydrogen is also called oxidation, and the addition of hydrogen is called reduction, even if no oxygen enters into the reaction at all.

The student must be patient with the recall of these elementary facts, for they lead to an important idea in the understanding of the biochemistry of the cell, namely the perpetual tug-of-war between oxygen and hydrogen, between oxidation and reduction—a tug-of-war whose result depends on the relative strength of the two sides. An oxidising agent is one that will readily give up oxygen, or

will take up hydrogen, or do both. Its presence will strengthen the oxidation processes in its neighbourhood, whether one side of the tug-of-war is weakened, or the other strengthened, or both. A reducing agent will have the opposite effect. It may further be noted that each atom of oxygen is as strong as two atoms of hydrogen, so that the neutral point is water, H_2O, which is neither an oxidising agent nor a reducer. This neutrality of water is not to be confused with its neutrality in another sense, that it is made up of the ions H and OH, thus balancing between acid character on the one hand and alkaline on the other.

Lavoisier's great contribution was the idea that living implies oxidation, or, in other words, combustion; but whenever we think of the cell as like an internal-combustion engine, a difficulty arises in regard to the temperature. The burning of an organic compound in the air evolves great heat, which is inconceivable for a living cell. And if we picture the less complete oxidations that are often brought about in the laboratory, we see that these require powerful agents, such as nitric acid or chromic acid, which would irreparably damage the living cell, even in small quantities. Or again, if we think of very quiet oxidations, such as rusting, where the iron combines with the molecular oxygen in the air, these take place very slowly, whereas the oxidations in the cell are very rapid. We see then that the idea of the combustion of the living body is far from being easy; the facing of the difficulty is leading, however, to a deeper understanding of the chemistry of the cell.

The first point to be noted is that oxygen may momentarily exist in what is called an *active state*, as free atoms, especially at the instant at which it is liberated from some compound; and this active oxygen will readily oxidise substances which resist ordinary molecular oxygen, and will do this at a low temperature.

The second point is the importance of *catalysis*, which is the alteration of the speed of a reaction by some "foreign" substance which does not enter into the products that result, and so thereafter is found unchanged. Especially important in connection with the cell-combustion problem are those catalysts which speed up such reactions as oxidations which would otherwise proceed very slowly. In ordinary chemistry it is well known that spongy platinum serves as a catalyst in the oxidation of sulphur dioxide to sulphur trioxide, and finely divided nickel serves as a catalyst in the reduction of unsaturated oils by molecular hydrogen. In many cases, as in these two, the catalytic agents have very large *surfaces*, on which the reaction they further has probably its seat. So what catalysts has a cell?

It is characteristic of the cells of plants and animals that they possess, and therefore presumably form, catalysts of a peculiar and important type—the *ferments* or *enzymes*. It is impossible to

obtain these substances in a pure state; they are probably allied to proteins, but their chemical composition is unknown; they are destroyed by heat; they form colloidal solutions in water. We may be pardoned for repeating that the colloidal state is one in which the dissolved substance exists in the form of very minute particles or droplets, and has therefore a very large *surface*, which is no doubt of importance in the activity of the enzyme. As examples of enzymes may be mentioned those of the digestive juices, which are formed in the cells lining the alimentary canal and its glands, but act *outside* the cell on the nutritive substances that have passed into the stomach or the intestine, or, in Invertebrates, into outgrowths of the food-canal such as the pyloric cæca of starfishes. As we have noticed in connection with "Digestion" (*q.v.*), the digestive juices include enzymes which split proteins into amino-acids, others which attack starch and complex sugars, others which work on fats. The function of one and all is to simplify the foodstuffs to relatively simpler forms which can be absorbed by the cells lining the food-canal, whence, in higher animals, there is a diffusion into the general blood-stream. But it must be understood (1) that there are similar enzymes that remain *within* cells, and do their work there; and (2) that some of the ferments serve to hasten chemical reactions very different from simplifications, for example, oxidations.

Asking again for a little patience in order to reach an appreciation of a great discovery, we must linger for a little over oxidising enzymes. There are two well-known and widely distributed oxidising enzymes which have the power of attacking hydrogen peroxide (H_2O_2), and converting it into water and oxygen; but whereas the one, *catalase*, sets free the oxygen in inactive, molecular form, the other, *peroxidase*, sets free active oxygen, which is of great chemical potency. The relation of these enzymes to each other, and to the enzymes which oxidise other substances directly, is very difficult and not well understood; but it may be possible to give an intelligible picture of how they work, though it must, unfortunately, deal with the enzymes in milk, not with those in the living cell.

If there is introduced into milk the nitrogenous base called *xanthine*—near uric acid—it is immediately attacked by an enzyme which splits off from the xanthin molecule hydrogen in the active state. In other words, the xanthin is oxidised by the removal of hydrogen. The active hydrogen does one of two things: (*a*) it may combine with some other organic substance which it reduces; or, (*b*) if air be present, it may unite with molecular, inactive oxygen to form hydrogen peroxide. But milk also contains peroxidase, which attacks the hydrogen peroxide and sets free *oxygen* in the active state, and this oxygen combines either with the xanthine or with some other organic substances, which it oxidises. The function

of the first enzyme, Schardinger's xanthine-oxidase, is to transport hydrogen from the xanthine to some other substance; the action of the second enzyme, peroxidase, is to transport oxygen from hydrogen peroxide to some other substance. One sets free hydrogen in an active state; the other sets free oxygen in an active state.

It is highly probable that this is the sort of thing that goes on in the living cell with its oxidising enzymes. It is probable that catalase is present, acting as a chemical safety-valve, destroying the hydrogen peroxide if it should be formed in dangerous amount.

All this is difficult; but the essential point is that there are cellular enzymes which transport hydrogen and others which transport oxygen, and that oxidations will proceed most smoothly and rapidly when hydrogen peroxide is formed by the one and destroyed by the other. The whole system or cycle may be regarded as *an arrangement for changing molecular oxygen, as in the air, into the active state.* Here, then, seems part of the solution of the problem of cell-combustion.

But there are a number of substances, said to be *autoxidisable*, which readily combine with ordinary oxygen from the air, i.e. molecular oxygen, and this without the aid of enzymes or great heat. One of these, very widely distributed in living organisms, was isolated by Gowland Hopkins in 1921, and is called "*glutathione*". It is a compound of three amino-acids (cystein, glycine and glutamic acid) and contains sulphur. It exists in two forms, the oxidised and the reduced, and it can change from one to the other while in the cell and under natural conditions. In the reduced form the sulphur is united to hydrogen, so that the formula may be written

$$G - S - H$$

It is oxidised by losing hydrogen, so that two molecules join together

$$G - S - S - G$$

and two molecules of active hydrogen are liberated. These probably go to combine with oxygen, forming hydrogen peroxide (H_2O_2), which in turn is attacked by peroxidase and yields active oxygen to aid in the burning or combustion of energy-yielding substances in the cell. But at the same time the oxidised glutathione can also further this burning by taking away hydrogen from the materials of the cell and returning to the reduced form.

Here again is a system or cycle in which oxygen from the air is made available for the oxidation of food-materials, and this is at the same time hastened by the removal of hydrogen. In the continuous cycle of change between oxidised and reduced glutathione, supplying oxygen by removing hydrogen, there is no need for the help of enzymes; but it is likely that the reactions are assisted by a

catalytic agent which is not an enzyme, namely, *iron*, which is represented in all cells, and probably aids greatly in their oxidations.

Perhaps it may be said that all this is too chemical, and not biological enough. Yet the discovery of glutathione is of the highest biological interest. Under certain conditions in the cells of plants and animals this substance reacts with the oxygen of the air, and is able to pass this on to bring about the oxidation of food-materials on which the supply of energy depends. It is the presence of this "*oxygen-transporter*" that makes combustion possible within the living cell at a temperature much lower than that of the burning candle. This was our problem, and part of the solution is summed up in the term enzyme and part in the word glutathione.

In 1925 Keilin discovered in many kinds of cells another substance that is capable of combining with the oxygen of the air and transferring it to the protoplasm. But this time it is a pigment to which has been given the name *Cytochrome*. It is allied to the reddish pigment of the blood (hæmoglobin) and it is significant that its molecule contains iron.

The Internal Pressure of the Cell.—Familiarity with cellular structure is apt to dull us to the physiological problems it presents, as in the multitude of units which retain their relative independence even when closely integrated, which absorb and lose fluids without necessarily becoming swollen or shrunken, and which so often have a substantial strength, although they may consist chiefly of water, as in the stem of a succulent plant. Minute compartments with delicate walls enclosing a complex mixture of materials in a colloid state, the seat of diverse chemical reactions which are often very rapid and intricate—microscopic systems with no little differentiation, such as is expressed in nuclei, centrosomes, and mitochondria—how do all these retain their stability? There must be a constant and delicately adjusted balance of conflicting strains and forces; and as an illustration of these we may take the conditions regulating the internal pressure of the cell.

In the first place, the contents of the cell have an osmotic pressure, due to the fact that there is a strong solution in water of organic substances and mineral salts. If we prepare a pot of porous clay, and bring about within its pores a deposit of a layer of copper ferrocyanide, we obtain a semi-permeable membrane; that is to say, a membrane which will allow certain materials to pass through, but not others. In the simple case we have chosen, the membrane will allow water to pass through; but it will prevent the passage of, for instance, molecules of cane sugar dissolved in the water. If the semi-permeable pot of clay be now filled with sugar solution and immersed in pure water, it is found that water enters the pot through the walls, tending to dilute the solution within. The level of the liquid

inside the pot rises above the level of the pure water outside, and accordingly there is a higher pressure inside than out, as expressed by the extra "head" of water. This "osmotic" pressure finally reaches a constant value; which depends on the strength of the solution, and the nature of the dissolved substance. It is now generally recognised that the external surface of the cell has to some extent the properties of a semi-permeable membrane; and we therefore find within the cell an osmotic pressure, if the medium in which the cell is bathed is a relatively weak solution. The pressure within the cells may serve to make them rigid by turgor, as is seen in many plant tissues. If the external medium of the cell be a relatively strong solution, water will pass from within outwards, and the cell will shrink. These alterations of osmotic pressure are important in connection with the rapid movements of some of the parts of plants, such as the leaves of the Sensitive Plant. It must be noted that the external membrane of the cell is peculiar in its behaviour when compared with artificial semi-permeable membranes. We cannot at present quite re-describe in terms of artificial semi-permeable membranes what the living cell is able to do in the way of allowing certain dissolved substances to pass through, while barring the way to others, for the livingness of the membrane makes a difference which can as yet neither be explained nor ignored.

Secondly, there is within the cell a pressure—normally much less mportant than the first—which is due to the tendency of colloidal jellies, such as form the framework of the cell, to take up water by "imbibition". This is comparable to the swelling up of dry gelatine in water and to the swelling of the jelly that buoys up the frog's spawn in the pond.

Thirdly, the cell has an internal pressure due to surface tension. There is always a tension at the surface where a liquid meets another liquid with which it does not mix, or at the surface where it is in contact with the air; and the effect of this tension is to make the surface smaller. It is this force of surface tension that makes water fall from a slightly open tap in droplets instead of in a continuous thin stream. At the surface of the cell there is a tension, the effect of which is to make it contract; and this is the third way in which a pressure is maintained within the cell.

THE ENVIRONMENT OF THE CELL: THE PERMEABILITY OF ITS MEMBRANE.—So far we have been considering the cell as a little world in itself, but this view is to be corrected by the picture of the cell as an area in the larger world of the body. So we naturally pass to the relations between one cell and another, and to the relations between a cell and the ambient fluids of the body, notably—in Vertebrates—the lymph.

The property of forming a film at its surfaces is one of the most

important characteristics of protoplasm. We have seen that a dye may diffuse freely within the cell, and that the ions of salts are similarly free; this is a definite indication that the many constituents of living matter which are soluble in water are prevented from being washed out of the cell by the presence of a membrane at the surface, through which they cannot pass. This property, it must be noticed, is seen not only in whole cells, but in isolated drops of protoplasm; a surface newly formed by injury quickly acquires a protective film. It is also reasonably certain that some at least of the various inclusions in the protoplasm, especially vacuoles, and probably the nucleus and the mitochondria, are bounded by somewhat similar intra-cytoplasmic films.

Microscopic examination and micro-dissection give us some information about these surface films, but let us consider first the more patent features of the surface of various kinds of cells. In the first place, there may be a wall or pellicle outside the cell, which does not form part of the living matter. Plant cells, for example, are characteristically confined within a firm wall or porous box of the complex carbohydrate cellulose. Many of the Protozoa, such as Paramœcium, and many ripe egg-cells, are invested with a pellicle of some unknown material outside the living matter; in a few cases (e.g. *Amœba verrucosa*), it may be remarkably firm and tough. On the other hand, there may be within the boundary of the living matter a zone of protoplasm different from the central cytoplasm of the cell; this is best seen in some unfertilised eggs (especially of the starfish) and in Paramœcium and other Protozoa. This *cortex* or *ectoplasm*, as it is called, is jelly-like and much stiffer and more solid than the central protoplasm, from which it also differs in certain physiological details. The actual protoplasmic surface film is distinct from both the external and internal elements described, and lies between them, at the boundary of the living matter. It cannot be seen, under the microscope, to have any apparent thickness, yet it is firm enough to resist gentle manipulation; while if it is slowly torn it forms again with sufficient rapidity to heal the wound at once. But if the film is sharply torn with the micro-dissecting needle, its delicate structure is interfered with and collapses not only at the point of injury, but presently round the entire cell: whereupon the contents of the cell diffuse out into the surrounding water and are scattered. The strength of the film varies in different cells and under different conditions.

The general interpretation of this film is that it forms a semipermeable membrane; that is, a membrane through which some molecules can pass while others cannot. An artificial membrane of copper ferrocyanide, for example, is permeable to water, but not to cane-sugar molecules in solution in the water; although the explanation of this property is still unknown. In many ways the cell mem-

brane behaves like a semi-permeable membrane of this type, as was shown by de Vries in his experiments on *plasmolysis*. The water within the cell is always a solution of various salts and soluble organic compounds; suppose then that a cell is immersed in pure water or in a weaker solution (a solution with fewer dissolved molecules in a given volume is said to be *hypotonic*), a change will take place; water will pass from the weak solution outside to dilute the stronger solution inside. The physical reason for this cannot be discussed here; it is enough to say that two solutions have so strong a tendency to equalise any difference in strength between them, either by diffusion of the dissolved molecules, or, if this is not possible, by movement of the water from the weaker to the stronger, that water will enter the cell from the weaker liquid outside till there is a considerable pressure (*osmotic pressure*) within. This pressure or turgidity is of great service in maintaining plant-cells in a more or less rigid state. Their cell walls are strong enough to withstand the pressure, but a red blood corpuscle immersed in a weak solution will take up water till the cell membrane bursts and the contents (the red pigment hæmoglobin) will be scattered into the water; this is known as "laking" the blood.

If, on the other hand, a cell is immersed in a strong (*hypertonic*) solution, water will pass from the cell to dilute the external fluid, and the cell will be seen to shrink; this is the phenomenon of plasmolysis studied by de Vries. Cells, or plants and animals generally, differ in their power to survive such changes of the osmotic properties of their environments. In general, it is found that the body fluids of marine Invertebrates have much the same osmotic pressure as sea water; they are isotonic. It is a remarkable fact that the salts present in these fluids, and indeed also in the blood of vertebrates, show much the same relative proportions as in sea water; but within the cells there is typically much more potassium and much less sodium than in sea water. This fact, that cells take up some salts in preference to others, is a clear indication that the picture of the surface film of protoplasm as a semi-permeable membrane must not be looked on too simply.

About the beginning of this century, Overton made a series of experiments on the permeability of the cell surface to various substances, and found that those which entered the cell most easily were organic compounds soluble not so much in water, as in the "fat-solvents" such as benzene, ether, and the fats themselves. Most of them had a narcotic influence on the cell. He therefore supposed that the cell membrane was composed of fat-like substances, lipoids; and this view has always had much to commend it. Nevertheless it is at the best too simple a theory to explain all the known facts.

Before considering later theories of the nature of the cell surface

or further experimental data, it may be useful to note a few general physiological considerations. It is quite evident that a large number of substances must enter or leave intact cells. Food-materials, including the sugars which do not dissolve in fat-solvents, oxygen, and water must obviously enter into all living cells, and carbon dioxide, water, and nitrogenous waste-producers (nearly all insoluble in fat-solvents) must pass out. It is evident also that the cells of the alimentary canal and the kidneys allow large quantities of salts to pass through their surfaces. In the kidneys, the alimentary canal, the lungs or gills, the capillaries of the circulatory system, permeability problems are clearly of great import.

It is curious that it is often hardest to demonstrate the permeability of the cell to the very substances which, on general grounds, must pass in and out. Overton, for example, believed that inorganic salts were quite incapable of permeating through the membrane, but it is now clear that this is not so, although their passage is undoubtedly slow; in any case, a theory which led to such a result was clearly proving too much. It is evident on general physiological grounds that salts do enter cells, though it is not possible to say why certain salts enter more readily than others. Another great difficulty in the problem is the fact, which seems to be well established, that salts may pass through cell membranes in one direction and slowly or not at all in the other. This "one-sided permeability" cannot be reproduced with any artificial membrane; and the various theories advanced to explain it (they largely depend upon a relation between the electric charges of the colloidal particles of protein within the cells and the ions of the salts, known as the "Donnan equilibrium") are difficult, and not wholly satisfactory.

A leader in this field was the late Jacques Loeb, and one of his most striking contributions to the subject is expounded in his papers on "balanced salt solutions". It is known that the properties of the surface film of protoplasm are influenced by many factors, the permeability being increased by injury or death, and also after the fertilisation of the ovum or the stimulation of irritable tissues; it is also known that the nature of the salts in the external medium is of importance. It is found that a certain concentration of solution of sodium chloride is sufficient to kill cells; but that this is not merely due to the solution being so strong (hypertonic) that a fatal degree of plasmolysis ensues, is shown by the fact that if it is made even stronger by the addition of an amount of calcium chloride, the cells survive. In some way the calcium salt counterbalances or "antagonises" the sodium salt, though the solution is even more hypertonic than before. Such a mixed salt solution is said to be "balanced", and sea water is a balanced salt solution. The idea, of such an antagonism between sodium and potassium salts on the one hand and those of calcium and magnesium on the other, is of

great importance in physiology, and is reflected in studies of the effect of these salts on the contraction of muscle, the beating of cilia, and so on.

In the field of permeability the recent work of Chambers is very important; it seems that sodium attacks the cell membrane, making it too permeable, while calcium salts have the opposite effect, and prevent either of the salts from entering at all. But if these salts are injected into the cell, by means of the micro-dissection apparatus, so that the cell membrane does not interfere, the result shows that calcium is the more deadly to the internal protoplasm. From without, however, it is unable to exert this action.

To return to the theories of the surface film: the theory of the lipoid membrane was followed by a theory of a protein membrane (for proteins have a great power of forming surface films). This again was followed by an ingenious theory of Clowes (1916), who showed that a film of lipoid containing droplets of watery fluid as an emulsion might very readily change to an emulsion of droplets of lipoid in a continuous watery fluid. In the first case substances soluble in water would pass with great difficulty; in the second case more readily; and it appears that the antagonistic effects of sodium and calcium on such a film are to sway the balance from one state to the other, so that sodium increases permeability by making the watery phase continuous, with only droplets of lipoid, while calcium reversed this effect. In many other ways, Clowes's hypothesis has been found to agree with the facts.

The essential facts are that certain gases, especially oxygen and carbon dioxide, certain organic substances soluble in fat-solvents, and water itself, enter cells with considerable readiness, while salts or other substances enter so much more slowly that for a time at least the membrane is almost semi-permeable and comparable to the artificial copper-ferrocyanide membrane, and osmotic pressure may be observed. On the other hand colloidal particles, which are of more than molecular size, do not pass through the film at all; where they do enter cells, it is by the engulfing or swallowing process called *phagocytosis*, and this applies also to solid insoluble granules. Lastly, it must be noted that the surface of the cell is far from being an unalterable datum; it may be affected in various ways; thus its permeability may be increased by diverse factors, by the interpenetration of external substances, and by injuries due to internal intruding organisms.

BUILDING UP AND BREAKING DOWN.—Characteristic of the living organism, illustrated, for instance, in the familiar contraction of muscle, is the simplification of large compounds into lesser ones, a process often accompanied by oxidation, but not always. The hexose-phosphate of the muscle-cell gives rise to the

simpler lactic acid, and this in turn to carbon dioxide and water. So, in a very different connection, the digestive juices simplify the complex carbohydrates to sugars with six carbon atoms (glucose); they break up the insoluble fats into two soluble portions (fatty acids and glycerol); and they split the protein food into the simpler amino-acids. The chief reason for the simplifications that go on in the alimentary canal is that the lining cells are not able to absorb large molecules or colloidal particles. These splittings belong to the class of reactions called hydrolyses: when the complex molecule is split in two, a molecule of water is also divided into H and O-H, and the "open ends", so to speak, of the broken molecule are "plugged" with the ions or loose atoms derived from the water. Many substances can be hydrolysed in the laboratory with the aid of strong acids or alkalies; but in the body the action of enzymes is all-important.

Protein molecules are so complex that the number of possible different proteins is almost infinite, and every species of organism has its own proteins. Foreign proteins, from a different species, introduced into the blood, may in certain cases have a serious effect. This, then, is another reason why the proteins are simplified to amino-acids in the intestine before being absorbed into the blood.

When the amino-acids are distributed to the cells they are again built up into proteins suitable for and characteristic of this particular organism. This is an example of the reverse process to breaking-down, it is a building-up or *synthesis* of complex molecules from simple ones; another example already studied is the formation of sugar from lactic acid. Two points about syntheses may be noticed: first, they are, as one would expect, usually accompanied by the reappearance of the water used up in the simplification process; second, they are usually expensive processes—they do not take place of themselves, but require supplies of energy. Thus the lactic acid concerned in muscular activity is transformed to sugar by sacrificing a fraction to furnish energy.

But an exception to this second point deserves some notice. Many chemical reactions are under certain conditions incomplete. When a fatty acid and an alcohol are brought together, they combine to form an ester; but the reaction stops before all the fatty acid and all the alcohol have been used up; only a certain percentage of the total possible amount of ester is formed. In the same way the ester can be split up or hydrolysed to fatty acid and alcohol, but not completely; a certain amount of ester will remain. The reaction is a reversible one, it proceeds in both directions; but at a certain concentration of ester, of acid, and of alcohol, an *equilibrium* is established between the two processes, and there is no further change in the concentration of the various substances unless the conditions of the experiment are altered in some way. The ester-forming

reactions are influenced by catalytic agents, in some cases by special enzymes; but the action of a catalyst is to *hasten* only. It does not matter whether we start with pure ester or with acid and alcohol, in the presence of a catalyst the equilibrium position will be reached more rapidly than before, but it will not be passed. So that under different conditions the same enzyme may aid either the formation or the breaking down of a compound molecule. This fact is generally true of enzymes: that their action is reversible. In reactions of this kind, the process of attaining the position of equilibrium, from either side, is a process which yields energy. Enzymes have no power of supplying energy to drive a reaction in the "wrong" direction; Bayliss aptly compared them to a lubricating oil which enables a weight to slide downhill (converting potential into kinetic energy) more swiftly and more easily, but has no power to help the weight to go uphill. We may think of a reversible reaction as V-shaped, with the position of equilibrium at the bottom.

The energy-yielding reactions within plant or animal cells, as we have seen, are first and foremost of the nature of oxidations, e.g. the conversion of lactic acid to carbon dioxide and water in the case of muscle. Animal cells generally have no power to reverse these reactions, because they have no form of energy available to "push the weight uphill". But exactly these reactions *are* reversed in the life of the green cells of plants, which from carbon dioxide and water form sugars, starches, and fats. It has been already noted that cells cannot get rid of their waste nitrogen in the form of the pure gaseous element, but only in the form of simple compounds; in the reverse processes, plants (with the exception of certain bacteria) are unable to start with pure nitrogen, but are able to build up simple nitrogenous products (nitrates and so on) into complex amino-acids and proteins. These reactions can only go on if energy is supplied to them, and the source of this energy is the sun.

The reactions themselves are by no means clear, and it is even less certain how the green pigment, chlorophyll, plays its certainly essential part. What is certain is that with light and chlorophyll, the plant cell can form sugar from carbon dioxide and water, the former obtained from the air, the latter from the soil. It is generally agreed that the first step is the reduction of the fully oxidised carbon atom of carbon dioxide to formaldehyde; it is likely that at the same time water is oxidised to hydrogen peroxide. The formaldehyde may possibly appear in an "active state" in which its molecules readily join together to form molecules of sugar. These reactions can be imitated to some extent in the laboratory if ultra-violet light is substituted for ordinary daylight, and it is conceivable that the chlorophyll is able to convert one kind of light into the other. But this question is discussed in another section along with the chemistry of chlorophyll.

In summary, it may be pointed out that two contrasting processes take place in the plant: (*a*) the transformation of complex molecules into carbon dioxide and water, with consumption of oxygen and evolution of energy; and (*b*) the predominating process of the conversion of water and carbon dioxide into complex molecules, with the evolution of oxygen and the consumption of the energy of sunlight. In animal cells, except in one or two green Protozoa, or in those which harbour symbiotic green Algæ, the latter process does not occur. Once a certain stage is reached, however, where syntheses take place unaccompanied by reduction, as when sugars form glycogen in animals or starch in plants, or when amino-acids form proteins, plant and animal cells become much more alike in their properties. Some power of synthesis is characteristic of all cells, a particularly important example being the synthesis of enzymes, of which we know almost nothing save that it must occur.

Summary on Cell-chemistry.—In what has preceded we have briefly considered some of the fundamental properties of living matter, such as its irritability and contractility, its power of secreting and growing; and the central fact about the chemistry of living matter is that it does not display these properties unless it is in a *partially oxidised* condition. In typical cells this condition is brought about by contact of the protoplasm with oxygen; and there are constituents of the protoplasm which are particularly able to unite with molecular oxygen and to pass it on to less readily oxidised constituents. The final products of the oxidation of organic compounds are carbon dioxide, water, and simple nitrogenous substances. To replace the materials used up in these reactions animals ingest food and green plants synthesise organic compounds from carbon dioxide and water, using the energy of sunlight in so doing. Processes of building up and breaking down of organic molecules go on in the cell, partly by way of preparation for the energy-yielding oxidation reactions, partly to form specific substances which the cell makes use of either as reagents (enzymes, pigments, glutathione, and so on), or to repair or enlarge its own structure in growth and reproduction.

There are, indeed, living cells which flourish in the absence of oxygen. In the higher animals which have adapted themselves to this mode of existence the essential reactions of the cell are incomplete combustions of organic material. Among anaërobic bacteria are those which are concerned chiefly with nitrogen, with sulphur, and with iron. Most important are those symbions which form nodules on the roots of leguminous plants and are able to convert the gaseous nitrogen of the air into organic nitrogen-containing compounds which the plant can make use of. In these cases it may be difficult to demonstrate that the energy of the cell is derived from oxidations, though in the widest chemical sense of that

elastic term it is probably true. In any event these cases are too exceptional and too little understood for further discussion here.

A difficult point in the chemistry of cells is the amount of chemical activity which goes on in certain cells, such as the red blood corpuscles of birds, which do not seem to have anything to show for it. They do not contract, they are not specially concerned in the receiving of stimuli, they do not grow nor form special substances as far as we can tell, yet they consume appreciable quantities of oxygen and food material. Warburg has suggested that the cell requires a constant supply of energy to maintain an essential ultra-microscopic structure within the protoplasm—possibly something of the nature of a film net. For chemistry this is a convenient idea, as it is difficult to see how so many different reactions can go on in a single cell in the absence of partitions of some sort; while the surfaces of such partitions might very well be the site of the reactions. It has already been pointed out that the network visible in stained and fixed cells is the unnatural result of very artificial treatment; and also that to the micro-dissecting needle protoplasm is apparently structureless and fluid. Moreover, if a dye be injected into the cell it spreads rapidly through the whole, and the fact that protoplasm conducts electricity is a sign that metallic and acid ions of the dissolved salts always present have an equal freedom of movement. It is possible that reactions in cells go on chiefly at *surfaces*, e.g. between "pure" protoplasm and its inclusions, like granules and vacuoles and mitochondria; on the external surface of the cell; on the surface of the nucleus, and so on; and that between these is a surrounding ocean of inactive protoplasm permeable to dyes and salts; nor is it impossible that to maintain such surfaces energy is required. It is certain that an injury to the cell causes the external membrane to become less efficient. Surface is undoubtedly of great importance in reactions within the cell, and protoplasm, like any other complex colloidal system, has a great tendency to form films at surfaces; hot milk is an extreme case of this property of colloids.

Warburg has, in any case, won a leading place in the study of the relation between the activity and the structure, whatever it is, of the cell. If cells are ground up and destroyed mechanically, without interfering with their chemical constituents (if this is possible), the structureless living matter continues for some time to consume oxygen and yield carbon dioxide; but enormously less than in the intact cell, and only in the presence of some more or less solid fragments. This is further evidence for the importance of surfaces in the chemical life of the cell.

RHYTHM OF THE CELL —It is in some cases evident that the dominant metabolism of a cell does not proceed continuously, but

in alternating periods of anabolism and katabolism. Thus a gland cell becomes loaded or charged with the preliminary stages of the characteristic secretion, and then it is unloaded or discharged, in some cases almost explosively. Attempts have been made to make the facts clearer by using analogies. The cell becomes surcharged, just as a Leyden jar with its store of electricity; and just as the charging of the Leyden jar is attended with effects conducive to dissipation and retardative to further transfer, so in a general way it may be with the living cell. Yet Prof. J. Joly, in his *Abundance of Life*, argues very convincingly that the analogy breaks down badly. For "the transfer of energy into any animate material system is attended by effects conducive to the transfer, and retardative to dissipation". Thus the young leaf growing in the sunlight utilises certain of the rays acceleratively; the more it gets, the more it grows, and the more it can take. "The organism is a configuration of matter which absorbs energy acceleratively without limit, when unconstrained!"

Another analogy has been found in inorganic chemistry. Ostwald has shown that one of the best known of all reactions, the evolution of hydrogen gas from an acid that is dissolving a metal, may proceed intermittently. "Fast" and "slow" periods quickly succeed one another. It seems that this is not due to the metal becoming temporarily "passive"—that is, protected by the formation of a thin film of oxide; and that it is not due to the metal or the acid becoming too highly saturated with the evolved gas. The cause remains obscure; but it is possible that the phenomenon may eventually throw light on the fact, or widely accepted fact, that the chemical reactions within a living cell proceed not continuously, like the movements of a turbine, but rhythmically, in a series of "explosions", like the engine of a motor-car. It may be noted that according to the modern "quantum theory" the energy emitted from a system or absorbed by a system, is emitted or absorbed not continuously, but in little bundles, parcels, or quanta.

An attempt has been made by J. L. Sager "to explain inherent rhythmicity as a physicochemical consequence of the colloidal structure of protoplasm". Living matter has the physical properties of a viscous, colloidal, emulsoid liquid. Owing to the viscosity of the living protoplasm there is a definite resistance offered to the discharge of energy. Owing to the unstable architecture of the protein molecular aggregates, what is called "trigger" action will set free a definite quantity of energy during katabolism. Then follow endothermic anabolic stages, in which the molecular architecture is reconstituted. Therefore katabolism and anabolism must occur in alternation and intermittently; they cannot proceed side by side or continuously. Hence "vital" rhythms.

Perhaps the general idea will be clearer if we give Mr. Sager's

picturesque illustration. In a stream there are two lock-gates, kept in position by powerful springs. The water accumulates above the gates till it drives them open. After the water has rushed through, the springs will come into action again and close the gates. Then the same sequence will be repeated. So is it in the discharge of energy in katabolism. "The molecular aggregates in the suspended, ultra-microscopic spherical droplets of colloidal protoplasm, hold a definite amount of energy which can be liberated by the 'trigger' action. The continuous liquid phase of the living protoplasm will have its dissolved substances in the gaseous state; and, presumably, molecular aggregates of such complex substances as proteins could not possibly be so held. It is because of this fact that it is the disperse phase which is supposed to be the seat of the molecular aggregates of special architecture, holding definite quantities of potential energy solely as a result of such architecture." The aggregates of molecules break down in katabolism and liberate energy, the liberation being in opposition to the resistance offered by the viscous protoplasm. Then anabolism comes into play, and the special molecular architecture, with its definite quantities of potential energy, is once more reconstituted. Therefore, the discharge of energy *must be* intermittent; the see-saw of anabolism and katabolism *must* continue rhythmically. We do not suppose that Mr. Sager has said the last word on this difficult question, but he has opened up an interesting line of thought; and its ideas can be extended from the fundamental autonomic rhythm, illustrated by the lock-gates, to superimposed rhythms which are correlated with external periodicities, like those of days and seasons.

VITAL STAINING.—It is now generally recognised that a microscopic preparation of a living tissue may be a very misleading thing; profound alterations in structure and appearance are inevitably caused by the (chemically speaking) rough handling which the living cells receive. First of all, the living matter, semi-fluid and never wholly stable, is "fixed" or violently solidified and probably distorted by powerful chemicals, such as picric acid or corrosive sublimate. Then, perhaps, the water is driven off by alcohol. The alcohol is removed, and the block of tissue immersed in melted paraffin wax. When this has cooled, it supports the frail cellular structures and allows the knife of the microtome to shear off thin regular "sections"—a hundredth of a millimetre or less in thickness. The paraffin is dissolved away when the sections are safely fixed to glass slides, and the process of staining, more or less complex, follows. It remains to drive off the water again and mount the stained sections permanently in balsam or some other preservative.

Such prepared sections can tell us much of the structure of tissues, for they are easy to decipher; but, as models of the *living* cells, they must not be trusted too far. Many attempts have been

made to study living cells under the microscope by the "dark-ground" or ultra-violet-light methods—or, simplest of all, by staining the living cells.

With this last method, striking results have been obtained, special dyes revealing special structures within the cell in an unambiguous manner. To discuss these here is impossible; but there are points in the theory of vital staining which deserve attention.

In order to stain the interior of the cell, the dye must be able to penetrate the impalpable membrane which forms the boundary of the cell. According to Overton's famous theory, now quarter of a century old, and not yet displaced though regarded as insufficient, this membrane consists of lipoid or fat-like substances, and a dye which dissolves in such substances can readily enter the cell; and this, indeed, is generally found; but some stains quite insoluble in lipoids may be accepted by the cell, especially in certain cases, such as the cells of parts of the kidney, which are specialised for the purpose of removing foreign substances from the blood. Here it is supposed that the uptake of the lipoid-insoluble dyes is an active physiological process (since it disappears if the cells are depressed by narcotics), while the lipoid-soluble dyes enter passively, seeping in by diffusion as they would into a droplet of oil.

Other theories of the action of vital stains are not lacking; they invoke the internal acidity of the cell, or the magic word adsorption; but, true or false, the "lipoid" theory outlined above is generally found helpful in trying to think clearly in regard to vital staining.

TISSUE CULTURE.—Our conception of the life of the organism must include the remarkable fact that isolated pieces of tissue may continue living away from the body altogether. A single nerve-cell may live and grow in a suitable culture for a week or more, and a fragment of tissue may be cultivated *in vitro* for years! Indeed, if care be taken to secure for the isolated fragment appropriate food, a supply of oxygen, a suitable temperature, and aseptic conditions, there seems to be little in the way of limit to its continued vitality in a glass tube, or on a glass plate, or in some other such arrangement. The life of isolated fragments of tissue from a chick embryo has been prolonged for ten years—a longevity not less than that of the hen into which the embryo might have grown! Throughout all that time there was growth as well as life, and the growth-rate was practically uniform throughout.

Undifferentiated tissues, whether embryonic or malignant, continue to proliferate *in vitro* with little histological change or none at all. They simply give rise to other cells like themselves. More specialised tissues often show extensive cell-division, even when this is not their usual behaviour in the intact adult animal, but ultimately they sink into an indifferent or embryonic type. They

exhibit *de-differentiation.* In certain cases the less specialised elements in a culture become cannibals as regards de-differentiated elements, that is to say, the relapsed descendants of cells that were originally specialised.

The tissue-culture method practically owes its origin to Prof. Ross Harrison, who made pioneer experiments with isolated nerve-cells in 1910; it has been ably developed by Carrel and others, and it has great possibilities. It makes it possible to distinguish the potentialities that are resident in the tissue itself in a normal culture from the reactions that follow the introduction of drugs or extracts of other tissues, or hormones, or extracts of malignant tumours. It is a quaint technique, but it may enable investigators to detect or delimit the factors that control, restrain, inhibit, or stimulate the growth of tissues. It is one of the methods by which descriptive embryography is gradually being advanced into causal embryology.

How Long Can a Cell Live?—A "Big Tree" or Sequoia may live for over three thousand years, but much of the tree, namely, the hard wood and outer bark, is merely dead skeleton. From the continuance of the life of the organism as a whole one cannot argue to the longevity of particular cells, except in cases where no replacement occurs and the individual cells remain alive. Thus it is generally believed that when the brain of a backboned animal has once reached its normal size, there is no further multiplication of its nerve-cells; therefore, a living nerve-cell of that brain has lived since the animal's maturity at least. It is generally believed that there is no increase in the number of our brain-cells after birth. If this is quite correct, then those nerve-cells of a centenarian's brain that remain alive must have lived for a hundred years. The American botanist, D. T. MacDougal, has recently pointed out that the cells of the pith of the tree cactus (*Carnegiea gigantea*) may continue to grow and function for more than a century. It does not seem to be the living matter or protoplasm that grows old in a cell; it is rather what may be called the furniture of the cell-laboratory, that is to say, the more stable plasmic framework within which metabolism occurs. Thus, if a cell is not very highly differentiated, it should live longer than one that is specialised. As for single-celled organisms, which divide periodically, it seems that many of them must have evaded natural death altogether.

The Physical Basis of Life.—Huxley used these words, "the physical basis of life", as a sort of definition of protoplasm or genuinely living matter. While there is "one kind of flesh of men, another flesh of beasts, another of fishes, and another of birds", Huxley was laying emphasis on the fact that all kinds of "flesh" have a similar physical basis. Speaking of the structural units or cells that build up the body of plant or animal, von Mohl said in 1846: "The

remainder of the cell is more or less densely filled with an opaque, viscid fluid of a white colour, having granules intermingled with it, which fluid I call protoplasm." The word was invented, we believe, by Purkinje six years before, but perhaps von Mohl was the first to use it as a general term for the kind of material that goes to the making of all kinds of living creatures.

But, as already said, the modern student would change some of von Mohl's words. Instead of opaque, he would say clear; instead of white, he would say colourless; instead of viscid, he would probably say jelly-like or colloid. The fact is that protoplasm shows itself as a liquid in which there are suspended multitudinous minute particles, occasionally, especially in plant cells, in a state of constant ("Brownian") movement. When the protoplasm dies the liquid "sets" as a jelly, and the Brownian movement of the particles ceases. A similar change from "sol" to "gel" often takes place temporarily during life. Everyone is familiar with the coagulation of white of egg in boiling water, or with the liquefaction of gelatine in similar conditions; but the changes in protoplasm are naturally somewhat subtler. Raw white of egg can be partly solidified at a low temperature and entirely solidified by drying; and it is possible to work the change the other way by raising the temperature again or by adding water. But protoplasm can pass from the solid to the liquid, from the gel to the sol, or vice versa, without any change in the temperature or in the water-content.

Before saying more about the physical characters of protoplasm, let us think of it chemically. Living matter cannot be analysed as such, for the methods of analysis must kill it, and death may mean that large molecules rapidly tumble down into smaller ones. But the chemist tells us that there are no elements in the protoplasm that are not common enough in the adjacent non-living world; it is a question, not of the presence of rare elements, but of the combinations of common ones. The chemist also tells us that the dead protoplasm shows a mixture of proteins, carbohydrates, and fats besides minute representation of some other materials. It is well known that proteins are never absent, and it follows that they must play an essential part in the chemistry of life. Proteins contain carbon, oxygen, nitrogen, and hydrogen (in that order of percentage), and usually a minute representation of sulphur. Examples, already stated, are the albumin of white of egg, the vitellin of yolk of egg, the casein of cheese, and the gluten of wheat. The protein molecules are very large and complex, sometimes consisting of thousands of atoms, and there are so many different kinds that it is safe to say that every distinctive type of animal or plant has some peculiar protein, characteristic of itself. The red colouring matter of the blood—the hæmoglobin—is a protein, and we know that this pigment in a dog is appreciably different from that which

occurs in a horse or a man. One has dreams of perfect diagnoses of species which will begin with a formula of the particular kind of protein and end with an appreciation of the creature's psychical mood, if it has got the length of having one.

But to return to elementary chemistry, the particles of protein and other organic compounds are present in multitudes in the liquid medium, and there may be crowds of immiscible droplets as well; and all this multitudinousness of minutiæ means a very large development of surface in proportion to the total mass. This allows of a great intensity of changes, because the area of surface is so enormous. Thus there is usually an electric charge on the contact surface between any two phases, e.g. a complex solid particle and a complex liquid medium; and the multitudinousness of the sometimes quivering particles—quivering because bombarded by the restless molecules of the fluid—means a large surface and therefore a more copious spring of electrification. It seems that many of the marvellous properties of living matter, such as rapidity of chemical change, are wrapped up with this colloidal state, which means that multitudinous particles and droplets are suspended in a complex medium.

In the laboratory of a cell there is often a production of chemical substances that cannot be regarded as being very intimately connected with the living matter itself. Thus a cell may make granules of a black pigment (melanin) or crystal-like spangles of guanin, and all such things must be regarded as side issues, away from the essential metabolism. Now, if we could subtract from the total of the cell-substance all these by-products, there would be left the genuine living matter. In technical language, cytoplasm *minus* metaplasm equals protoplasm. This is theoretically clear, but practically impossible. The probability is that there is no one substance which should be called protoplasm, but rather a co-ordination of proteins, carbohydrates, fats, and other stuffs which work into one another's hands in a very effective way. There is much to be said for using the metaphor of a firm; the partners are effective in themselves, but the characteristic efficiency is due to their correlation. But while a common purpose is the bond that keeps the firm together, acting as a successful unity, we do not know what the bond of union is in a cell. The persistent self-preservative activity of protoplasm is much more difficult to understand than the suicidal explosion of the gunpowder. In the protoplasm there is for a time a succession of up-building, constructive, or anabolic processes. But the clock that is thus wound up is ready to run down; and thus there is a succession of disruptive, destructive, or katabolic processes. These two sets of processes, winding-up and running-down, make up the metabolism of protoplasm; and it is characteristic of life that the see-saw can be kept up for days or years or

stretching cycles of years. The living organism is a going concern; its accounts balance.

Perhaps the greatest change of recent years in our picture of protoplasm is that implied in the abandonment of the view that it has a microscopically demonstrable structure, network-like, fibrillar, or otherwise. The appearance of intricate structure has often been seen under high magnification in fixed and stained cells, and many beautiful drawings of the protoplasmic reticulum have been published. But this microscopically demonstrable structure is an artefact; it does not exist in living cells; it can be mimicked in white of egg. Protoplasm is a liquid emulsion, mostly consisting of water; but it can be as firm as a jelly-fish is firm, and it can make for itself a supporting framework. But when we speak of protoplasm as structureless, we must hasten to add that it is a "film-pervaded or film-partitioned system". The living cell is partitioned by extremely delicate films with diffusion-hindering properties, which allow dissimilar chemical processes to occur in contiguity; but these partitions are not usually demonstrable in any direct way.

Protoplasm as Psychoplasm.—So much then here for protoplasm as physical basis of life. So far we have been thinking of it as the physical basis of physiological life. Yet since the germ-cells and the fertilised ovum cannot but carry along with them, concealed amid their simpler developmental potentialities, a psychic life, up to the level of their species, we are thereby already thinking of protoplasm as also the basis or bearer of psychical life. And if so, after all our enumeration of physical and chemical processes and physiological functions, there is no escape for us, as evolutionary life-students, from also wondering and searching, as best we can, for such plasm-elements and characters as must be already present, however latent, in the very Amœba or the ovum, and which bear the promise and potency of psychic life; as from simplest irritability to sensing, and thence beyond, even to complexest developments of human faculties, and from vaguest contractility to highest deed. Here, then, inevitably arises the conception of protoplasm as also something of psychoplasm, since bearing with it possibilities of ever fuller and completer evolution of life, and this in both its main aspects, the organic and the psychic, in animals and in ourselves. And since all the tissues of a developed animal body are more or less in organic touch with its neural elements, as these with their centres, we see no way of refusing to these their psychic tinge as well. Does not this conception indeed aid us, as towards understanding the unified organisation of the body in health, the pain and disease which arise with undue abatement of this unity, and even the *vis medicatrix Naturæ* in convalescence and recovery—so plainly the renewal of unity of functioning, both organic and

neuro-central, i.e. physiological and psychological together; as every skilled and cheering nurse is ever helping to re-establish?

We are thus not here seeking to separate organic and psychic life; on the contrary, despite the intellectual convenience—and often the practical necessity—of looking at life's forms and manifestations by turns from the physiological point of view and from the psychological as well, we are ever seeking to realise their unity; without which body is but corpse for post-mortem examination, while mind or psyche vanishes beyond our experience or recall.

We can neither fully accept Descartes' view of "animals as automata" nor the essentially kindred presentment so ably and experimentally argued for by Loeb and others; for we hold their "mechanistic dogma" as but a half-truth, a perspective of physiological value so far as it goes, but at once due to and limited by the mechanistic advance so characteristic of our times. Nor can we fully follow W. McDougall through his ably argued case for Animism; and we must postpone for a subsequent chapter an outline of that doctrine of psychophysical Interaction—say, rather, interaction of Biopsychosis and Psychobiosis in vital and rhythmic unity—which is the best that we can offer. So enough here to recall the illustration of the convex yet also concave aspects of a circle or other curve; for on each aspect we can so far specialise in geometric thought, as for chords within and tangents without; yet thereafter and more clearly harmonise all we have separately learned.

But this commits us to a frankly panpsychic view of organic life; and even for plant as well as animal: and why not? From the familiar life-experience of sleep, with its lapse from consciousness into the sub-conscious, to the subtle and fertile investigation of this latter which has been one of the most noteworthy advances of the past generation or more, we no longer see any reason for refusing that something of psyche to the plant-world as well, which child and woman, poet and mystic have ever granted to tree and flower. We no longer see a Dryad inhabiting the tree; that poetic vision corresponded to the dualism of separate body and psyche which neither biology nor psychology confirms: but we do see the tree as itself the Dryad; since growing, breathing, moving, and sensitive to light and more—sensitive, as Darwin long ago showed for his insectivorous plants, beyond the utmost limits of our own conscious sensibilities. Other investigators have confirmed these subtleties of plant-life, and Bose yet further experimentally demonstrates and extends them, so that in what seems the most slow and gentle of all organic movements, his multi-millionfold experimental magnification shows an energy of growth in rising pulsations which give an impression of urgency of life-effort, as vivid as can be those of animal life to ordinary eyes. Conspicuous movements, as of the sensitive plants—when all is said for their physical processes, and

for hormones said to be present also, show some equivalent of neural process, and after stimulations such as we know as readily of sensory character: while again the integration of each plant as a characteristic whole, despite the frequent modifications impressed by external environment, presents a unity which we cannot conceive as simply organic without something of psychic as well. Protopsychic though that may be, who can say more for the chick within the egg, or even for the unborn child?

Sleeping and sub-conscious though such life be, must we not realise—as experimental studies of sleep, hypnotic state, etc., all tend to show—that the sub-conscious state is consistent with a certain measure of what we cannot but call sensing, experiencing and feeling—surely even of proto-emotional thrilling, sub-ideative urging, and so in animal forms with neuro-cerebral and proto-psychic changes and interactions, towards definite behaviour and consciousness later? Without some such continuity and association of incipient neural functioning with its psychic equivalent, how can we imagine the needed and obvious organic and psychic functioning of maturer life at all?

Before reading anything of the modern psycho-analyst's library, with its exposition of the sub-conscious, and this even to its substantial identification of the Hindu mystic's ideal of "Samadhi" (and perhaps that of the Buddhist's Nirvana also) with the placid bliss of sleeping infancy, even unborn, it was of no small interest to find, on long rides with Bose through Himalayan forest-glades and flowers, that on our different lines of scientific reasoning, as well as in speculative ways, we had alike come to the same conception as that so often expressed in Western poetry, and in Hindu religion and philosophy as well—of plant-growth and flowering as at once expressing the organic health and fullness, the beauty and even the ecstasy of Life, perfected and at one.

COLOURS AND PIGMENTS

Coloured substances or pigments of many kinds play a manifold part in the life of organisms. In some cases, indeed, they may be called essential, as in the green pigments of plants and the red pigment of the blood of backboned animals. Apart from pigments there may also be great utility in colour; thus it is useful to the ermine (*Mustela erminea*), to the mountain-hare (*Lepus variabilis*), to be white in winter; but there is no pigment involved in the whiteness. Conversely, some important pigments, such as the cytochromes involved in oxygen control, contribute little or no colour to the tissues in which they occur.

WHAT COLOUR MEANS.—It is not possible to understand colour

without some acquaintance with the theory of light; but our outline must be very brief. From such a source of energy as the sun, radiations rush outwards through space in waves of varying length from crest to crest. The waves of X-rays, used in radiotherapy, or the waves of ultra-violet light, also used to promote health, are very short, while those of heat rays, and still more those used in broadcasting, are increasingly long. But all have the same velocity, approximately 186,300 miles per second. If the whole vast range of electromagnetic radiations be compared to a series of sixty-two octaves, one octave would include those rays to which our eyes are sensitive, the limited range which we call visible light. It must be noted, however, that the range is not quite the same for all animals with eyes; thus ants, as Sir John Lubbock first showed, are sensitive to ultra-violet light, which is invisible to us.

The octave of ordinary visible light is itself made up of rays of different wave-lengths; and each of these produces in our eye and brain a particular colour-sensation, such as red or green. The shortest are the violet rays, familiar at one end of the spectrum or in the rainbow, which have a wave-length of some forty millionths of a centimetre, and the longest, at the other end, are the red rays, which are twice as long as the violet. A blend of what we might call all the notes of the octave produces *white* light.

The colours, which are the vital results of the rays of different wave-lengths, may be for convenience written down in this way:

Violet	Green
Indigo	Yellow
Blue	Orange
Green	Red

The pairs which are here placed opposite each other in this arrangement were named by Chevreul "complementary colours", and their relation to one another is significant in understanding colouring. If by some process of filtering we subtract from the complete white light any one member, for example, red, then the balance will be disturbed, and the light will no longer appear white, but *green*—the colour complementary to that which was filtered out. The filtering may be effected in various ways. Thus a sheet of copper will remove much of the white light that falls on it, and will reflect chiefly the red—whence the familiarly pleasant colour of burnished copper. Yet if the sheet of copper be so thin that light can pass through, then the red rays are *absorbed*, and the filtered light will appear green. Solutions of copper salts, such as we may see in the great globes in the druggist's shop-window, have a fine blue colour, which is due to the fact that the ions (or wandering detached atoms) of copper have the power of absorbing light at the red end of the spectrum. This filtering is of fundamental biological importance, since

the screen of green pigment in the green leaf means that the orange-red rays of the sunlight are absorbed, and they are the rays that are useful in photosynthesis. It may be mentioned that some "light-filters" are exceedingly delicate in action, blocking out accurately a particular series of wave-lengths, so that sharply edged dark bands are seen when the filtered light is analysed in the spectroscope. The presence of a particular chemical element in the source of the light may readily be detected in this way. Other filters, however, are somewhat diffuse in their action. It is understood, then, that a coloured substance is one which interferes in some way or other with the whiteness of ordinary light.

This interference may be due to the *physical state* of the coloured substance, as when a finely grated surface, or one from which the light is reflected at two different levels, "interferes" with the light and shows colours, often of an iridescent nature. Everyone knows that there is no pigment in the wall of a soap-bubble, which nevertheless shines with all the colours of the rainbow. Similarly, there is no pigment involved in the beautiful iridescence of mother-of-pearl. In such cases we may speak, therefore, of physical or structural coloration.

But while such structural colour is not uncommon, it is not so common as pigmentary colour, which is due to a property of the molecule of the substance in question to absorb or to reflect only certain parts of the visible spectrum. Such substances, occurring in plants and animals, are called *organic pigments,* and they may be of the most varied chemical nature. It is not yet possible to suggest a consistent theory connecting particular kinds of chemical composition or structure with the particular colours to which they give rise; yet it is of great interest to inquire into the nature of organic pigments from the chemical side.

Classification of Colours in Organisms.—Before we pass to the chemistry of organic pigments it will be useful to give examples of the different kinds of coloration that are illustrated by living creatures. (A) Structural or physical coloration, due to the texture or architecture of the surface, may be illustrated by the mother-of-pearl layer in the interior of a mollusc's shell, where the lime is laid down, along with organic cement (conchiolin), in very fine laminæ, one over another. If the pearly shell is pounded in a mortar, the result is powdered lime. All the iridescence is gone, for it depended on the laminated structure; only whiteness is left, and that is due to the almost perfect reflection of the white light from the multitudinous surfaces of the chalky powder. In the same way the beautiful colour of a white Narcissus is due, not to any pigment, but to reflection from very numerous sap-vacuoles among the cells of the perianth: so if we compress the white petal between finger and thumb it becomes transparent.

(B) Chemical or pigmentary coloration, due to the presence of a substance whose molecules absorb or reflect only a certain part of the visible spectrum, may be illustrated by the green colour of most plants, the reddish pigment of our blood, the blackish pigment of dark fur, and the yellowish pigment of yolk of egg.

(C) But the finest coloration, in animals at least, is due to a combination of physical and pigmentary colour, as in the blue feathers of some parrots, the metallic green wing-cases of some beetles, the beautiful blue scales of some butterflies, and the iridescent bristles of Aphrodite, the sea-mouse. When physical structure is a factor accessory to pigmentation, the colour of the surface changes as it is moved about, as is familiar in peacock's feathers: when physical structure enhances the effect of a pigment, it may result in a colour, notably blue or green, which is quite different from the colour of the pigment. With this introduction let us now pass to consider pigments in their chemical aspect.

Chemistry of Organic Pigments.—This study is relatively modern and it is still in the early stages of its development. Excellent pioneering work was done many years ago in Krukenberg's *Vergleichend-Physiologische Studien* and *Vorträge* (1881–1889), but his followers, such as Sir F. Gowland Hopkins, have not been many. An admirable introduction to the subject is furnished by Dr. Marion Newbigin's *Colour in Nature* (London, 1898).

Chlorophyll Pigments.—It is convenient to begin with chlorophyll, the green colouring matter of plants, for it is the most important pigment in the world, being vitally connected with photosynthesis. The molecule of chlorophyll is still very imperfectly understood, but it is readily split into two parts by the action of an alkali. One of the parts is a complex, colourless alcohol called phytol. The other part has for its foundation the pyrrol ring (C-C-C-C-N), in which four carbon atoms form a ring with one atom of nitrogen. In chlorophyll there are four of these pyrrol rings joined together, and linked to these in some way there is a single atom of magnesium. The reason for giving this detail is that a very similar structure recurs in the red pigment of the blood! As a matter of fact the chlorophyll of plants is much more complicated than used to be supposed; it is indeed a system of four pigments. Two of these, chlorophyll-*a* and chlorophyll-*b*, absorb the red and orange rays and therefore appear green. Besides these there are two yellowish pigments, carotin and xanthophyll, which seem to be less important. When the light shines on the green leaf, there is probably a continuous cycle of change, from chlorophyll-*a* to chlorophyll-*b*, with absorption of carbon dioxide, and then back again from chlorophyll-*b* to chlorophyll-*a*, with liberation of oxygen. This is of great interest, because in the blood of Vertebrates the red pigment shows the same general alternation—between oxy-

hæmoglobin, formed at the place of oxygen-capture, in gills or lungs, and hæmoglobin which has parted with oxygen at the seat of combustion, such as the muscles.

There seems to be no more difference between chlorophyll-*a* and chlorophyll-*b* than there is between hæmoglobin and oxyhæmoglobin; in both cases the latter contains more oxygen. Both the chlorophylls absorb red and orange light, and therefore appear green. Very different from the chlorophylls, but similarly related to one another, are the two yellowish pigments, carotin and xanthophyll, to which we shall return. How chlorophyll and its associated pigments join in the process of reducing carbonic acid and building up carbon compounds, from formaldehyde and sugar upwards, is still uncertain; and the problem is discussed under the heading photosynthesis. It is enough here to mention the certainty that chlorophyll combines with carbonic acid.

BLOOD-PIGMENTS.—As a convenient second group we may rank the blood-pigments, notably the red pigment hæmoglobin, which is characteristic of Vertebrate animals and occurs in some Invertebrates as well. Earthworms and many seaworms have, in a general way, the same blood-pigment (hæmoglobin) as man, and so have the larval stages of the Harlequin fly, popularly known as "blood-worms". The last instance is interesting since these larvæ live in stagnant water that has less oxygen-content than usual, and hæmoglobin excels all other blood-pigments, such as the hæmocyanin of most crustaceans, in its capacity for entering into a loose union with oxygen. The "blood-worm" illustrates physiological adaptation.

As we have mentioned, hæmoglobin is remarkably like chlorophyll in several ways. Its molecule is even larger, and again it may be split into two parts. But the colourless portion in this case is not an alcohol, but a protein called globin. The coloured portion, now called *hæm*, again consists of four pyrrol rings linked together with an atom of metal, which in this case is not magnesium but iron. These resemblances are striking. Unlike chlorophyll, which is the same in all green plants, hæmoglobin varies from one animal to another, but these differences concern not the essential nucleus (hæm), but the attached protein (globin). It is a fine illustration of *specificity* that when the hæmoglobin of different kinds of animals is made to crystallise, the blood-crystals show differences. Even in nearly related species, such as horse and ass, or dog and fox, there is a difference in the details of the hæmoglobin crystals. In fact, there is an example of a chemical basis of species of which we shall afterwards see more.

Although hæmoglobin shows an alternation of gaining and parting with oxygen, its functions are very different from those of chlorophyll, and they cannot be related to the power of absorbing

light. In the lungs, where the blood is richly supplied with oxygen from the inspired air, the pigment in the red blood corpuscles forms oxyhæmoglobin; in the tissues of the body this reaction is reversed, and oxygen is set free to supply the needs of the living cells. In a somewhat different way the hæmoglobin helps to carry the carbon dioxide from the tissues to the lungs—that is to say, from the place of formation in combustion to the place where it is eliminated as poisonous waste. It may be noted that while the combination of oxygen with hæmoglobin is the commonest of our vital occurrences, there is something extraordinary about it; it is not strictly comparable to any known chemical combination. (See *Respiration*.)

There is a continual breaking-down of hæmoglobin in the body, and the products, freed from protein and from iron, are dealt with in various ways. Thus they almost certainly give rise to the bilirubin and biliverdin of the bile of Vertebrates, and some are laid down as tissue-pigments in various backboneless animals, such as leeches and molluscs.

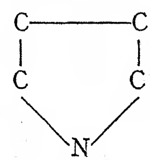
Allied to hæmoglobin, but less effective, are a number of other blood-pigments which have the power of combining temporarily with oxygen. Some of these are derivatives of hæmoglobin itself, in which the "hæm" nucleus remains intact. In many molluscs and crustaceans there is a very imperfectly known bluish pigment called hæmocyanin, in which there is copper instead of iron. The bluish colour is sometimes so pale that the blood appears colourless, though it is certainly not pigmentless.

A reference may again be made to an interesting series of pigments, called Cytochromes, discovered by Keilin in 1925. Cytochrome contains the "hæm" nucleus, and is therefore related to hæmoglobin, but it is much more widely distributed. It occurs in both Vertebrates and Invertebrates; it is abundant in the wing-muscles of insects. It also occurs in yeast and in certain bacteria, and also in flowering plants. It would indeed seem to be almost universal. Its function is discussed along with respiration, but it may be noted here that, like hæmoglobin, it has to do with oxygen. It apparently serves not to carry oxygen over a distance, as from lungs to muscles, as hæmoglobin does, but to control oxygen *within* the cell.

MELANINS.—A third set of pigments, with a wide distribution, is the melanin series. Their diverse occurrence may be illustrated by citing as instances the dark skin of the negro or the dark hair of the "Black Celt", the black feathers (apart from their structural metallic gleam) of the crow tribe, the black choroid which makes the dark chamber of the eye, and the ink-sac of cuttlefishes, which painters have long used for gloomy pictures, their sepia coming

from the sepia cuttlefish common in Mediterranean waters. But if painters use "sepia" now, it is synthetic, not cuttlefish sepia.

Of the chemistry of melanin little is known. The probability is that it is not a single pure substance, but often, at least, a mixture. It is very hard to purify, since it will not crystallise. It always occurs in minute granules, and it almost defies solution in solvents. Some biochemists have connected it with an amino-acid (i.e. next door to protein) called "tryptophane"; and in some cases this is very probable. Other biochemists believe that it is connected in some way, just as hæmoglobin is, and chlorophyll too, with the *pyrrol ring*, which, we may repeat, consists of four atoms of carbon linked to one atom of nitrogen, as may be represented by the symbol



But the general view in regard to melanin, a view that has passed beyond hypothesis, is that melanin is derived from tyrosine—an important amino-acid—or from some similar substance. The general interest of this will soon be apparent.

Pure tyrosine, in a test-tube, treated with a preparation of an enzyme or ferment of wide occurrence called tyrosinase, and then exposed to the air, becomes first reddish and finally black, and this black pigment is, as far as one can tell, identical with natural melanin. As tyrosine and tyrosinase are both of wide distribution, especially in Invertebrates, it is highly probable that natural melanin is formed by this reaction.

There is, however, a closely allied substance called by the long name dioxyphenylalanin and by the short name "Dopa", which is, perhaps, the first result of the action of tyrosinase on tyrosin. It blackens spontaneously, especially in contact with alkalies. It has been suggested that "Dopa" is the source of the melanin of Vertebrates, as in dark hair, dark feathers, and the black in the lining of the body-cavity of lizards, frogs, and many fishes. It is almost certain that "Dopa" plays a part in the blackening of the cocoons of many insects; and according to some it also occurs in some plants.

If melanins are derivable from tyrosine through the action of a ferment, the general interest of the fact is that tyrosine is an amino-acid, and that amino-acids readily arise by the breaking-down of proteins which are invariably present in living matter. Thus a common pigment may be interpreted as the result of a disintegrative or katabolic change in proteins.

Chromolipoids or Lipochromes.—This fourth group of pigments is widely represented both among plants and among animals. They are called "coloured fat-like bodies" or "fatty pigments", but they show no great resemblance to fats beyond their solubility in ether. The two yellow pigments, carotin and xanthophyll, which accompany chlorophyll, are common chromolipoids, and they also occur in many animals. Carotin gives the yellowish colour to butter and xanthophyll occurs in the yolk of the bird's egg. The chromolipoids are mostly reddish and yellowish pigments, and they occur in many brightly coloured birds and fishes, where they are often accompanied by melanins. The colouring matter of the yellow fat in many animals, such as some lizards, has a chromolipoid nature. Another good example is the reddish zoonerythrin ("animal red"), which is common in many of the higher Crustaceans, such as prawns and the Rock Lobster (Palinurus), which Victor Hugo called "the cardinal of the sea". It is a widespread pigment, occurring, for instance, in the red wattle above the eye of the grouse, and it is chemically next door to carotin of carrots. The blue colour of the common lobster is due to a compound of zoonerythrin with a protein. When the protein is destroyed by heating, the free pigment is left to give its familiar red colour to the boiled lobster. "And like a lobster boiled, the morn From black to red began to turn!"

There are many other animal pigments that cannot be included in any of the groups referred to, such as the uric-acid pigments of some butterflies' wings, the purple secretion of the dog-whelk Purpura and of some other Gasteropods (the animal counterpart of indigo), the red pigment of the cochineal insect (a distant counterpart of the alizarin of madder), but it is perhaps more important at present to emphasise the great classes we have mentioned—the chlorophylls, the blood-pigments, the melanins, and the chromolipoids. In other connections we shall refer to some of the others, such as the anthocyan of many flowers and of the withering leaves—the flowering of the forest.

Physiological Status of Pigments.—It would be a great gain in biological interpretation if we could be more definite in regard to the physiological status of organic pigments. Are they waste-products, or by-products, or reserve-products? Is there any way in which they may naturally arise in the course of the everyday chemical routine or metabolism? In animals, are they sometimes directly connected with the vegetable food? For if we can reach some security in regard to the primary physiological significance of a pigment, then we can proceed with more confidence to inquire into (*a*) its internal utility in the life of the body, and (*b*) its external survival-value in the struggle for existence.

It is contrary to true scientific method to hurry towards generalisations before sufficient data have accumulated, yet tentative

hypotheses may serve to prompt research; and it is not too much to say that there are some glimpses of light. Thus if melanins are derived from amino-acids, which are constituents of proteins, we may regard them as katabolic derivatives of these universally present components of protoplasm. Similarly, it is scientifically satisfactory when an animal lipochrome can be linked back to the carotin or xanthophyll of plants. The "flavone" or "flavonol" of the wings of the Marbled-white butterfly (*Melanargia galatea*) is probably derived by the caterpillar from the Cocksfoot or the Timothy grasses on which it feeds. Some pigments may be unhesitatingly classified as waste-products, such as the uric-acid pigments of some butterflies. The carmine that sometimes forms half of the weight of a female cochineal insect (*Coccus cacti*) is a glucoside, yielding sugar when treated with dilute acid, and may perhaps be interpreted as a reserve-product. Of others, it may be said vaguely that they are by-products of the everyday chemical routine (or metabolism) of the body.

USES OF COLOUR

The common kingfisher flying swiftly upstream like an arrow made of a piece of rainbow; the golden oranges amidst their glossy leaves; the newly caught herring, blue and green, silvery and red; the bluebells ringing by the wayside; the ripe cherries gleaming like cornelians; the purple heather on the moor; the poppies ablaze among the corn; the rubies and emeralds of the Bird of Paradise; the golden kingcups in the ditch; the deep scarlet of the Poor Man's Weather-glass; the azure of the Arion butterfly's wing; the subtle iridescence of the worn shells wetted by the incoming tide; the daring display of the parrot; the elusive browns of the brooding woodcock—what does it all mean, this long gamut of coloration? A joy for ever, of course; but this narrow human point of view, though by no means unreasonable, is not satisfying.

We have seen that certain pigments, notably chlorophyll, hæmoglobin, and cytochrome, have a primary physiological significance of the utmost importance, and that others, like the dark melanins, the ruddy lipochromes, and the green pigment of the bile, have a primary physiological significance as by-products or waste-products of the chemical routine (or metabolism) of the body. Their presence is readily accounted for, and we can then proceed to discover secondary utilities, such as protection or decoration. Similarly, it is instructive to note that the fine lines that make superficial interference-gratings and the delicate laminæ of a mollusc's shell are expressions of orderly rhythmic growth. In many cases growth must proceed on a line-upon-line plan; in many cases

there is bound to be a zoned structure. The cross-bars on a hawk's feathers express diurnal fluctuations in the blood-pressure during the period of development, and the fish keeps its annual diary in its scales. We cannot at present account for all the architectural peculiarities that give rise to structural coloration, but in many cases they are the ripple-marks of growth. We can thus understand why there should be what may be called raw material available for secondary utilisation as adornment or disguise. We have thus cleared the way for a study of the uses of colour.

In certain cases a dark colour may protect the animal from the glare of the sun, and this utility would not be in the least incon-

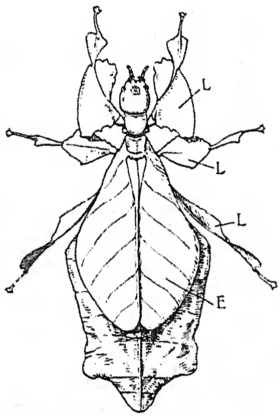


FIG. 51.

One of the Commonest Leaf-insects (Phyllium). From a specimen. The front wings or tegmina (E) are extraordinarily leaf-like, and the legs (L) have flat leaflet-like expansions which increase the protective resemblance. The colour of the adult insect is green.

sistent with the discovery of a physiological reason for the deposition of an extra quantity of melanin in the skin.

For a warm-blooded creature in very cold surroundings the dress that conserves most of the precious animal heat is a coat of white fur or white feathers, as in ermine and ptarmigan, but this is not inconsistent with the discovery of a physiological reason for the development of gas-vacuoles and the non-formation of pigment in the suit of fur or feathers that is put on when winter comes. Nor is it inconsistent with proving that the whiteness is of protective value in making the ermine or the ptarmigan inconspicuous against a background of snow.

Protective or cryptic coloration is certainly very common, but its life-saving value should be proved, not simply assumed. Not every case is so satisfactorily documented as that of the green

Praying Mantis on the green herbage, and the brown variety among the withered leaves. For in this case the protective value has been proved up to the hilt and statistically measured, which is certainly not yet true of the white winter dress of the mountain-hare among the snow. The value of colour in supplying a cloak of invisibility is increased when the markings are also like those of the surroundings, as in the brooding woodcock, or when there are added possibilities of colour-adjustment, as in the flat-fish among the gravel. The climax is reached in cases of true mimicry, as when a palatable butterfly is the "double" of an unpalatable species with which it consorts.

Somewhat difficult, we think, are many of the cases of alleged "warning colours", where an unpalatable animal is very conspicuous, like a yellow and black salamander or a red and green burnet moth. The theory is that the conspicuousness serves as a noli-me-tangere advertisement, impressing itself on the memory of a forgetful enemy, saying, as it were: This gaily coloured creature is of no use, leave it alone. Of some such warning colours there is considerable experimental evidence.

On a firmer footing are the numerous cases where the bright colouring of the male animal contributes to the *tout ensemble* that interests or excites his desired mate. Among the bower-birds there seems to be a delight in brightly coloured objects, such as shells and pods, for their own sake—the dawning of an esthetic sense.

Sometimes the colours serve as advertisements of palatability, as in some insect-attracting flowers or bird-attracting fruits, but here again, in many cases, there is need for replacing surmise by precise demonstration. Thus, without denying that colour may have some attractive value to hive-bees, we are sure that the fragrance of the flowers is much more important.

The mention of flowers recalls another use of colour, what may be called a way-post function. As Sprengel indicated long before Darwin, there are often conspicuous spots on the petals of flowers which certainly look as if they might be of use in guiding the insect visitors to the nectar. It is not necessary to suppose that the insects would not find their way without the "honey-guides", but anything that prevents fumbling will tend to have survival value. The whitewashed stones by the footpath are not indispensable to the belated traveller, but they enable him to walk more rapidly and confidently.

Many nestlings have very bright colours inside their mouth, and Pycraft has pointed out that the conspicuousness of these, when the young birds gape, may enable the parents to supply the food with greater rapidity and precision. This may seem a trivial matter, but survival in the struggle for existence often depends on the difference between shibboleth and sibboleth.

We need not continue our illustrations of the uses of colour among living creatures, but we venture to reiterate the two points, that the first inquiry should refer to the primary significance of the pigment or of the architecture on which the coloration depends, and that the secondary significance of the coloration, if it has any, should be, as far as possible, demonstrated. In many cases, we venture to think, the colour has no use at all, but is purely incidental, as in withering leaves. Yet what a delight to human eyes!

THE EARTHWORM'S COLOUR.—As an instance of the familiar discovery that things are seldom so simple as they seem, we may refer to the redness of earthworms. What makes an earthworm red? Is it always blushing? Or is the skin so thin that the red blood shines through? And is there any use in its being red? It seems to have been securely established that the earthworm has in its blood the same red pigment, hæmoglobin, as we and all backboned animals have. But the red blood-pigment in the earthworm is in the fluid of the blood, whereas in backboned animals it is in the red blood corpuscles. This is an unimportant difference, however; for the earthworm and for man the physiological significance of the hæmoglobin is the same, it captures oxygen from the outer world—on the earthworm's skin, on the lining of our lungs—and surrenders it again to the tissues, where it is required to sustain the vital combustion that living implies.

But the redness of the earthworm's skin is not directly due to hæmoglobin; it is due to another pigment called porphyrin. And this requires just a word of explanation. Hæmoglobin is a combination of an iron-containing brownish pigment called *hæmatin* and a white-of-egg-like or protein substance called *globin*. But if the hæmatin in the blood be treated with strong sulphuric acid, the iron is filched away to make ferrous sulphate, and a pigment called hæmatoporphyrin is left. This pigment is also formed in the course of the everyday chemical routine of many animals, and it is not very unfamiliar, because there are traces of it in normal urine and quantities of it in some kinds of abnormal urine. Well, to come to the point, the pigment in an earthworm's skin is a porphyrin, but Kobayashi has recently shown that it is different from hæmatoporphyrin. The fact is that it is nearer to a porphyrin which can be derived from chlorophyll, the green pigment of plants. It is possible, then, that the redness of the earthworm's skin comes, not from the hæmoglobin of the blood, but from the chlorophyll in the vegetable remains on which the earthworm feeds. A porphyrin of this origin may be absorbed from the earthworm's food-canal by the blood, and then deposited in the skin. This may seem much ado about nothing, but it is a fresh illustration of the danger of thinking of things too simply. As to the use of the porphyrin in the earthworm race, it probably protects the earthworm from the

injurious effects of light, to which it is extraordinarily susceptible. This leads our thoughts to the origin of the earthworm's subterranean and nocturnal habits.

COLOUR CHANGE.—When a frog, normally of a greenish hue, is put into a dark moist box in a cold room, it becomes dusky in a few hours, and blackish in a couple of days. But if it be put in a whitened box in a warmish, well-lighted room it puts on a lemon colour. The darkening is due to the "expansion" of branched black pigment-cells (melanophores) in the epidermis and dermis. The opposite change is due to the "contraction" of the black pigment-cells to microscopic pin-points, and this brings into prominence certain yellowish pigment-cells (xanthophores) in the dermis. It is not certain whether a melanophore in a frog draws itself together

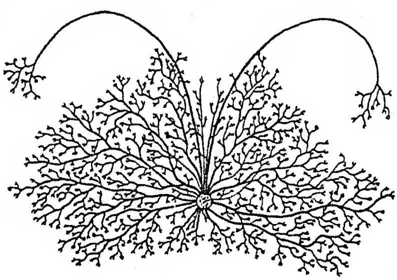


FIG. 52.

Complex Chromatophore from a Prawn (*Praunus flexuosus*). After Degner. The pigment flows out along the complex branches or contracts centripetally. This unusually complicated chromatophore appears to arise from a combination or syncytium of cells.

as a whole, just as if it were an Amœba, or whether the "contraction" means that the pigment granules flock towards the centre, as is certainly the case in crustaceans like the prawn. It used to be thought that the contraction or expansion of the pigment-cells in the frog was controlled by fine branches of the sympathetic nervous system; but the brilliant researches of Hogben and Winton have proved that the control is due to the hormone secreted by the pituitary body in fluctuating quantities. In reptiles, like the chameleon and the so-called "horned toad", there are superficial, yellowish, "interference" cells or xanthophores, and deeper melanophores with branches passing up into the outer layer. Most of the colour change is due to the up-and-down movement of the pigment granules in the melanophores, and this is mainly under the control of the adrenalin hormone secreted by the suprarenal bodies. In fishes, such as the plaice and the flounder—where the colour change is very rapid, the creature sometimes making itself invisible almost instantaneously—the control is effected by branches from the

sympathetic nervous system. Blind flat-fishes do not change colour. The message from the outside world affects the eye, then the brain, then the sympathetic nervous system, then the pigment-cells. There is sometimes an enveloping of the pigment-cell with the fine terminal branches of nerve-fibres, an innervation which has never been demonstrated in amphibians. Here, then, are three classes of vertebrates, and the predominant control of the colour change is effected in three different ways! It is possible, however, that there may be auxiliary controls. In crustaceans, like the Æsop prawn, the chromatophores are usually multicellular, and they often contain more than one kind of pigment, with different susceptibilities and rates of movement. There is a regular rhythm between practical transparency at night and expansion of pigment during the day, and this is due to the direct action of the light on the skin. On the other hand, a response of the crustacean to the nature of its background comes about through the eyes and the central nervous system, the important point being, not the intensity of the light, but the incidence of the rays. In cuttlefishes, which are molluscs, the chromatophores are little multicellular bladders, often visible to the naked eye, and surrounded by radiating muscle-fibres. The play of colour on an octopus is extraordinarily beautiful. There is evidence here that the central nervous system controls the colour change, but there is also strong evidence that the muscle-fibres of the chromatophores may respond directly to the light and differently to different wave-lengths. It is very interesting that there should be such variety of arrangement in effecting the same result, namely, the colour response of the animal to environmental change. A fine exposition is given by Hogben in his *Pigmentary Effector System* (1924). Where the control is effected by a hormone from the pituitary or the suprarenal, it will be necessary to explain how the environmental stimulus reaches such deeply seated organs from the superficial receptors.

ORGANIC LUMINESCENCE

It has been shown that with the contraction of muscle and the secretory activity of glands, with the closing of Venus's Fly-trap (Dionæa) and the collapse of the leaf of the Sensitive Plants, electrical changes are associated. In all vital phenomena there are probably changes of electric potential. But in most cases these electrical changes are not in themselves of importance in the life of the animal or plant; they are merely accompaniments or concomitants of the movement or the secretion. When, however, as in the Torpedo or the Electric Eel, there is a special and well-defined *electric organ* which can give a shock, useful in defence and

offence, then we must conclude that the production of electricity is important as such. The sub-function has become a main function.

The same holds in regard to the production of light by certain plants and animals, which are popularly and erroneously called "phosphorescent". It is very unlikely that the light given off by luminous bacteria, for instance, has any value in itself; but when a deep-sea fish shows a *luminous organ* with a lens and a dark envelope which restricts the emission of the light to one direction, we are naturally inclined to search for some use—though there are many cases where we cannot at present safely suggest what that use may be. We start, then, in our discussion of luminescence with the idea that in many cases the production of light may be an unimportant accompaniment of some essential metabolism, yet that the loss of energy in this direction has been over and over again independently utilised in the everyday life of the organism of the animal at any rate.

OCCURRENCE OF LUMINESCENCE.—Aristotle speaks of the luminescence of dead fishes and damp wood, which we now know to be due to bacteria and fungi respectively; and long before Aristotle the fishermen must have noticed that in the summer evening the oars sometimes drip sparks and the breaking waves may gleam with light, which we find to be mainly due to the stimulation of myriads of pin-head Infusorians called Noctilucæ. In warm countries the bush aflame with fire-flies must have been a familiar sight for ages, and among maritime peoples the "phosphorescence" of the fish hung up to dry could not escape attention. Yet the idea of light as a by-product either of vital processes or of complex organic substances is of recent origin. Indeed, there seem to have been only two important steps before the last quarter of the nineteenth century. In 1667 Robert Boyle showed that the presence of air is necessary for the luminescence of damp wood and dead fishes, an observation that practically proves (for us) that organic luminescence is of the nature of an oxidation. In 1794 the not less ingenious Spallanzani noticed that while dried parts of naturally luminous jelly-fishes cease to give out light, they do so once more if they are re-moistened. This proved that bio-luminescence is not necessarily bound up with vital processes, for it often occurs in organic substances which are discharged from an animal, or in materials present in part of a dead organism.

In his monograph, *The Nature of Animal Light* (New York, 1920), Dr. E. Newton Harvey of Princeton (whose names command respect!), gives a criticised list of the occurrence of luminescence in no fewer than thirty-six orders of animals. We say a criticised list, for it is necessary to exclude a number of misinterpreted cases. Thus the luminescence on the breast feathers of individual owls and some other birds is probably due to contamination by a

luminous fungus. The shining of the cat's eyes in the dark (though never in a really dark room) is merely an interesting reflection of faint rays from the highly developed tapetum, and is comparable to the shining of the luminous cave-moss (Schistostega), where certain lens-like epidermic cells act as reflectors. In a simpler way, a "luminous frog" had to be excluded from the list, when it was found to have gorged itself with fire-flies.

Although luminescence has been occasionally reported from animals living in fresh water, e.g. in the larvæ of a harlequin fly (Chironomus), and in those of a fire-fly from Celebes, Harvey will not admit that it occurs except on land or in the sea. Its well-documented occurrence in a few freshwater animals may be due to the ingestion or the adhesion of luminescent bacteria; yet this criticism, as we shall see, has proved a sword that has pierced the critic's own hand. For there are now many adherents to the theory that a large number of luminescent animals are luminous simply because they are habitually and heavily infected with luminous bacteria. In this connection we should notice the curiously *sporadic* occurrence of animal luminescence. For while there are classes, like the Ctenophores, in which all the genera and species are luminescent, it often happens that within a class only a few isolated types have this peculiarity. Thus while the boring-shell Pholas is one of the best-known cases of luminescence, it stands in this respect very much alone among bivalve molluscs.

Luminescence occurs in various Infusorians, like Noctiluca and Pyrocystis, and in some Radiolarians; in none of the Sponges; in numerous Stinging Animals or Cœlentera, such as Sea-pens (Pennatulids) and the Portuguese-Man-of-War (Physalia); in all the Ctenophores (which many zoologists would keep apart from the Cœlenterates); in sundry worm-types, including several earthworms (Photodrilus), but in no leeches; in isolated star-fishes and in not a few Brittle-stars or Ophiurids; in no Lamp-shells (Brachiopods); in no Moss Animals (Bryozoa or Polyzoa); in a multitude of Crustaceans, large and small; in two or three Myriopods, e.g. *Geophilus electricus*, one of the Centipedes; in numerous insects, especially among Elaterid and Lampyrid beetles; in no Arachnids (except a dubious Indian spider); in a very few Bivalves, like Pholas; in a few Gasteropods and Squids. In the large class of Tunicates there are only a few instances of luminescence, one of them the gorgeous free-swimming Pyrosome, which may be a yard in length and give light enough to allow the observer to read a printed page. There are many instances among marine fishes, especially among those that frequent considerable or great depths. As to plants, bio-luminescence is confined to Bacteria and Fungi; for the oft-quoted story of Linnæus' daughter seeing light from dittany flowers (Dictamnus) is not verifiable.

Luminescence in Fresh Water.—It is usually stated that luminescence never occurs in freshwater animals, but "never" is a dangerous word. Some years ago there was a well-documented account of a luminescent freshwater larva of one of the harlequin flies (chironomids); and K. G. Blair has recently published a description of the luminous aquatic larva of a Lampyrid beetle or fire-fly, allied to Luciola. The larvæ were collected in South Celebes from a mountain stream at an elevation of about 4,000 feet. The larvæ were seen as luminous points on the stones at a depth of about two feet, and are specially adapted for a life in streams. But the point is that they were luminous, so that's that!

Nature of the Light.—A body heated to a high temperature may give off light-waves, and we call it incandescent. But bioluminescence is the very opposite; it is "cold light", without any heat rays. It is altogether *visible* light, with no infra-red or ultra-violet rays. As Langley and Very pointed out in their well-known paper "On the Cheapest Form of Light" (1890), the luminescence of the fire-fly is all light and no heat—hence cheapest, in the sense that none of the energy is lost in non-visible radiations. The emission of light by bodies after previous illumination or radiation is called phosphorescence, but organic light is not of this nature; it is due to the oxidation of some substance produced by cells; it is a bio-chemical phenomenon. But it is important to recognise that organic light behaves like light from ordinary sources. As Harvey says: "Like ordinary light, animal light will also cause fluorescence and phosphorescence of substances, affect a photographic plate, cause marked heliotropism of plant seedlings, and stimulate the formation of chlorophyll."

Location of the Light.—In many luminescent animals the oxidisable luminiferous material undergoes its combustion within the living cells where it is produced. This *intra-luminescence* is illustrated by fire-flies, many small marine crustaceans, and Noctilucæ. It is also characteristic of all the luminous fishes save one, which will be described later on.

In perhaps the majority of luminous animals, however, the combustion of the luminiferous material occurs outside the body, it may be on the surface, or in the water, or on the ground. The material is exuded before it becomes luminous. This *extra-luminescence* is well illustrated by Pholas, whose secretion becomes brilliant outside the body; and as Dubois showed (1892) it may become luminescent when re-moistened after being kept in a dry state for several months. But this also holds true for the normally intra-cellular luminiferous material of glow-worms (Lampyris), which has been kept dry for ten months without losing its luminescent property when moistened (Bongardt, 1903). In some of the luminous Copepods the secretion does not become luminous until it is mixed

with the water; and here again Giesbrecht (1895) has shown that the material can be kept dry for weeks without losing its virtue. Jelly-fishes and sea-pens also illustrate the exudation of a secretion which shines on the surface of the body; and, to take a very different instance, one of the Myriopods (*Geophilus electricus*) leaves a luminous trail on the ground. It is convenient, then, though perhaps unimportant, to distinguish intra-luminescent and extra-luminescent animals.

LUMINOUS ORGANS.—When the light is produced from an exuded secretion, this usually comes from relatively simple glands, which may be diffusely scattered or definitely arranged. But in some of the instances of intra-luminescence there are very definite, often very elaborate, luminous organs, well illustrated in various fishes, higher crustaceans related to prawns, and in the fire-flies. Harvey lays an interesting emphasis on the fact that these organs are sometimes strangely like eyes. In front of the light-producing or

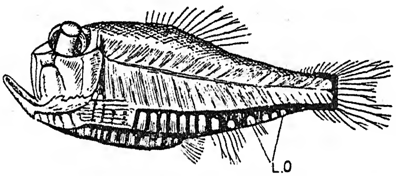


FIG. 53.

A Luminescent Deep-sea Fish (Argyropelecus), with numerous luminous organs (LO) on the lower parts of the body, and prominent telescope eyes. After Murray and Hjort.

photogenic cells there may be a lens, sometimes triple; behind them there may be a reflector; round the sides of the organ and behind the reflector there is often a dark envelope shutting off the light from the tissues of the animal itself; and, finally, there may be a nerve, stimulating and controlling. Now many an eye has its lens, its reflector, its pigmented choroid, and its optic nerve, so that there is often a very striking resemblance between an organ that produces light and one that perceives light. The probability is that the resemblance is one of "convergence", and that there is no homology between luminous organs and eyes. To solve analogous problems, e.g. of focusing and darkening, somewhat similar methods have been utilised in the course of evolution. No doubt there are deep differences between luminous organs and eyes. Thus, as Harvey puts it, the important transformation of energy in the former is *chemo-photic*, in the latter *photo-chemical*. The nerve of the luminous organ is of the stimulating efferent type, while that of the eye is sensory and afferent. At the same time, the resemblance between luminous organs and eyes is often striking, and it becomes quaint in cases like the Stomiatid fishes (Anomalops and

Photoblepharon), from the East Indian Archipelago, where the luminous organs can be turned inwards, obscuring their constant luminescence. This corresponds, in a way, to shutting the eye, which, however, in the absence of lids, no fish can do!

Theory of Bio-Luminescence.—About 1887, Prof. Raphael Dubois of Lyons University showed that a hot-water extract of the luminous tissue of the rock-boring Pholas very rapidly loses all trace of luminescence. A cold-water extract of the same remains luminescent for a longer time. But when the two extracts, which have both ceased to show any light, are mixed together, there is luminescence once more. These facts led Dubois to the theory that the hot water rapidly destroys a ferment or enzyme, *luciferase*, which acts on a photogenic substance, *luciferin*. In the hot-water extract the ferment had disappeared, and without the ferment the luciferin, unaffected by heating, could not produce light. In the cold-water extract the luciferase had acted on the luciferin and eventually oxidised it all. In short, the hot-water extract had luciferin without luciferase; the cold-water extract had luciferase which had used up all the luciferin in solution; a mingling of the two naturally produced light—*naturally*, if this theory is sound.

For many years Newton Harvey has been following the clue which Dubois discovered; and his general result is a confirmation of the view that bio-luminescence is the result of an energetic interaction between protein-like fermenting substances (*luciferases*) and photogenic substances (*luciferins*), which have much in common with peptones—the results of digesting proteins.

The three cases which have been most intimately studied are the fire-flies, the boring shell, and a small marine crustacean called Cypridina; and in these there is strong evidence in support of the conclusion that bio-luminescence is due to the interaction of luciferase and luciferin. It must be admitted that there remains considerable vagueness in regard to these two substances, which appear to differ in different animals, as is the way with proteins. The luciferase is gradually used up when it oxidises large quantities of luciferin, which would not be true of a typical enzyme or ferment, but its behaviour indicates something enzyme-like. One part of luciferase in 1,700 million parts of water will give light when some luciferin is added, and a similar dilution of luciferin will give visible light when luciferase is added. The probability is that luciferase is an organic enzyme or catalyst which oxidises luciferin, or accelerates the oxidation of luciferin, with the result that light is produced.

The Bacterial Theory of Bio-Luminescence.—Of recent years there has developed a very different theory of bio-luminescence, that it is due to partner-bacteria, and it is possible that both theories are correct. Certain cases of bio-luminescence may be *intrinsic* and

due to some peculiarity in the metabolism; others may be *extrinsic* and due to clusters of symbiotic bacteria.

Newton Harvey has made a detailed study of two East Indian fishes already mentioned, Anomalops and Photoblepharon. They are common off the Banda Islands and they have some peculiarities. Thus the large luminous organs give out light continually, night and day, and without stimulation. The investigator could not demonstrate luciferin and luciferase, but under the microscope he found in the luminous organs innumerable mobile bacteria, comparable to those that make dead fishes "shine in the dark". When the organ was dried and re-moistened, it gave only a faint light; *which is also true of luminous bacteria.* The light was extinguished without a preliminary flash when fresh water was added, *as is also true of luminous bacteria.* Moreover, poisons that put out the light of luminous bacteria had a similar effect on the light-organs of these two Banda fishes. So the suspicion grew into a hypothesis: that the luminous organs in these animals were incubators for the growth and nourishment of luminous bacteria living in partnership or symbiosis with the animals.

It may be asked whether it was proved that the bacteria observed were themselves luminescent; and the answer is in the negative. Yet this is not necessarily fatal to the theory. When the bacteria were isolated and made to grow by themselves in a jelly culture, they gave forth no light. This may mean that the theory is wrong, and that the light is produced by the metabolism of living cells in the fish. Yet it may only mean that the bacteria do not light up except in certain surroundings and with certain food. Further experiments are necessary.

We have already referred to the extraordinary Fire-flame or Pyrosome, a tubular colony of free-swimming pelagic Tunicates, brilliantly "phosphorescent" with greenish-blue light or with changing colours. A common size of colony is the length of one's hand; but it may grow to the length of one's arm, and one of this size will light up a dark room so that the furniture can be seen. The light is discontinuous, unlike that of the Banda fishes; and another difference is that the Pyrosome's light seems to require a stimulus, such as a collision with another animal or a splash from a wave. When one is kept in a quiet aquarium, it is brilliant for a while, and then the light fails. These three facts seem quite against the bacterial theory of luminescence. But the question is not so readily answered. When we look into the structure of a Pyrosome, we see a tubular colony of thousands of individuals, each of them with two luminous organs like little jewels. The cells of these spots include minute corpuscles like rodlets or horseshoes in shape, very suggestive of some forms of bacteria. The difficulty is to decide between the two interpretations, the one regarding

the corpuscles as luminescent partner-bacteria, the other regarding them as luminiferous granules belonging to the Pyrosome itself. The luminous organs of some cuttlefishes are complex eye-like structures, including a lens, a reflector, a dark curtain, and a central mass of light-producing cells. Inside the last Pierantoni finds myriads of bacteria, sometimes hunting in couples. These he regards as the source of the light. The subject has been carefully discussed by Buchner in his comprehensive book, *Die Symbiose*, and he comes to the conclusion that the luminescence of Fire-flies, Fire-flames, and Cuttlefishes—three very diverse types—is due to luminous bacteria which have entered into a partnership or symbiosis with the animals, whose luminescence is thus a borrowed splendour. This seems to us a sweeping generalisation, especially in those luminous animals that have an elaborate eye-like organ. In any case, the evidence cannot be called conclusive until the so-called bacteria are proved to be luminescent in some environment away from their dominant partner.

Uses of Luminescence.—When an organism simply exudes a luminous secretion or sparkles at numerous points all over its surface, it is quite possible that the luminescence is a by-play without any significance as such in the everyday life. As we have said, it may be comparable to the electric discharge associated with many vital processes. But this is not a satisfactory interpretation when there is an elaborate luminous organ. The search for a use is then imperative, but the suggestions that have been made remain more or less speculative.

(*a*) The light may serve as a lure, which attracts booty in the darkness of deep waters. This seems plausible when the luminous organ is near the mouth, notably when it dangles at the end of a fishing-rod-like fin-ray extended from the roof of the skull, as in some Anglers.

(*b*) The light may serve, on the other hand, as a warning, which scares away intruders or distracts predaceous molesters. It might be compared to what is called "warning coloration".

(*c*) The light may serve as a lantern, helping abyssal squids and fishes to find their way about. This idea is tenable when the luminous organ is situated in the vicinity of the head, which is often not the case. This interpretation would not apply to fixed animals like sea-pens.

(*d*) The light may facilitate the recognition of kin by kin, and serve as a sex-signal in mating. In fire-flies there appears to be an interchange of luminous signals between the more active males and the more sedentary females. It is noteworthy that the toad-fish, Porichthys, is luminous only during the spawning season.

It is evident that the chemical physiology of animal light has outrun the theory of its ecological significance. In all probability

we have to deal with a widespread peculiarity in metabolism, expressive of high intensity of life, which has been seized upon in different types for different uses and elaborations.

In course of his long and varied investigations into luminescence, Prof. Dubois has expressed the hope, in principle quite rational, that a mastery of its secrets, chemico-physical, bacterial, etc., may some day lead to practicable and highly economical utilisations for lighting purposes. It must be said that no less unexpected and remarkable applications of bacteriology and of biochemistry are already familiar to us, while others are in the stage of active inquiry. It is as yet but a dream, yet by no means a wholly absurd one, that from the ranks of such resourceful and untiring workers may yet emerge for us even rival companies of lamp-lighters, surviving by economy of energy over their predecessors; and why not even more pleasing too!

Special Case of Bio-Luminescence.—Of most luminous fishes three things may be said: (1) that their production of light must be of use to them, since it is associated with elaborate organs, often suggestive of eyes; (2) that their luminescence is intrinsic and not bacterial; and (3) that they are intra-luminescent, oxidising their photogenic material within the cells of the luminous organ.

To the last statement, a single exception is at present (1930) known, namely a fish called by the unprepossessing name Malacocephalus lævis, which might be translated "Smooth Softhead", surely not a happy name for a creature that, as we shall see, has almost succeeded in making a halo for itself. It belongs to the Macruridæ, a family closely allied to the Gadidæ, which includes cod and haddock, hake and ling. It is a common fish along the outer edge of the continental shelf from Ireland south to Morocco, and is taken in considerable numbers by fishermen who trawl for hake in waters of over 150 fathoms. A few small specimens struggle into shallower water off Galway and the Fastnet. There is nothing very remarkable in its appearance except the contrast between the very long whip-like tail and the short thick body. But its luminescence, discovered in 1925 by Mr. C. F. Hickling, is unique. (See *Journ. Marine Biol. Assoc.*, Oct. 1925.)

On the under surface of the "Softhead's" body there is the luminous organ which Mr. Hickling was first to notice. It consists of a folded or plaited area of glandular skin, which has sunk into the musculature of the body-wall, between and behind the pelvic fins. This area forms a compact gland with a flat wide duct, out of which there come at intervals little luminous clouds—the oxidation occurring outside the body. There is no evidence of the luminosity being due to bacteria living within the tissues of the fish; on the contrary, the evidence confirms the interpretation that luciferin is rapidly oxidised into oxyluciferin by a ferment luciferase. The

organ is embedded in the musculature, and it is by contraction of the muscles that the luminous secretion is shot out.

In reference to this special case, standing by itself among fishes, let us test the various theories of the possible utility of bio-luminescence.

(*a*) For some cases it has been suggested, as above, that the light produced by an animal may serve as a sex-signal, as in fire-flies and glow-worms. The toadfish (Porichthys) is luminous only at the breeding season. But the light of Malacocephalus is shared by both sexes, and the luminous organ was well-developed in the smallest specimens collected. Therefore the probability is that the sex-signal interpretation does not hold in this case.

(*b*) In some other animals, as in certain deep-sea fishes with the luminous organ dangling on the end of a rod rising from the top of the head, it has been not unreasonably suggested that its use may be to guide the animal in the darkness or semi-darkness. But one can hardly think of a lantern being stowed away on the under side of the body between the pelvic fins! It is not as if Malaco-cephalus were a motor-car, requiring a rear light.

(*c*) It has also been suggested that the luminescence of marine animals, especially sedentary and sluggish ones, may serve as a lure that attracts booty. Mr. Hickling thinks that this not unreason-able interpretation may perhaps hold in the case of the "Softhead". It feeds on crustaceans, such as small crabs, shrimps, and amphipods, and it is quite possible that they are attracted to the light. In this connection it is of interest to notice that one of the Banda luminous fishes, Anomalops, is used by fishermen as bait. But it does not necessarily follow that its value as bait is due to its luminosity. It is obviously difficult to obtain definite experimental evidence for or against these utilitarian interpretations.

(*d*) There is a fourth possibility, namely that the luminescence may confuse enemies, and this is the view that Hickling most favours for his Malacocephalus. Speaking of the musculature sur-rounding the gland, he says: "Contraction of these muscles would cause the secretion to be shot out, and its use would seem to be exactly analogous to the ink-sac of Cephalopods, but whereas the latter emit a cloud of ink, this fish emits a cloud of light."

Captain Jones, of one of the trawlers, reports that a large specimen of the fish, that was thrown overboard while still alive, emitted a cloud of fire, which spread "like a dinner-plate" and remained visible for some time. Thus a Malacocephalus pursued by a Hake may puff out its luminous secretion and at the same time change its direction. The Hake is confused or may pause to investigate the strange halo. Meanwhile the "Softhead" is far away. To other enemies the light may be alarming, and the result would be the

same. This seems a good working hypothesis for this particular case.

SUMMARY.—Bio-luminescence in animals is sometimes *extrinsic*, that is, due to the intense metabolism of luminous bacteria on the surface or even in the body. In some cuttlefishes, for instance, the evidence points to the conclusion that the luminous organ is a nest of symbiotic luminous bacteria; but the demonstration of this in cultures has not succeeded.

The evidence is strong that in the great majority of cases the bio-luminescence of animals is *intrinsic*, i.e. a part of the metabolism, sometimes slight, sometimes emphasised. In crustaceans like Cypridina, in Pholas, and in almost all luminous fishes the bio-luminescence seems unassociated with bacteria.

In fire-flies, the boring Pholas, and the small marine crustacean Cypridina, the experimental evidence is strong in support of the view that a somewhat protein-like ferment, luciferase, varying in different types, brings about the rapid oxidation of a somewhat peptone-like photogenic substance, luciferin, which changes into oxy-luciferin and in so doing produces light.

In one set of cases, e.g. sea-pens, Pholas, prawns, and the Malacocephalus above described, the photogenic material is oxidised outside the body (extra-luminescence). In the other cases, e.g. Noctiluca, small marine crustaceans, the photogenic material is oxidised *in situ* (intra-luminescence).

The uses of bio-luminescence are still very uncertain, but it looks as if a by-product, one might almost say by-path, in metabolism had been seized upon in the course of evolution and utilised in various ways—as a sex-signal, as a light to guide, as a lure for booty, or as a puzzling concealment or even perhaps as an alarming warning.

THE COLOUR OF THE HAIR.—As a special case of colour interest let us take the hair. There is a considerable range of colouring in the hair of mammals and of man, but it seems to depend almost wholly on there being less or more of a dark pigment called melanin. We include, of course, under "less or more" any inequalities in the distribution of the pigment in different parts of the body, or in different parts of the same hair, or at different times in the year or in the life.

A black cat has much melanin, a polar bear has little. Reynard the fox is midway between these extremes. But the colour of the hair almost always depends on the amount of melanin, which is also the skin pigment that makes the colour-difference between white, yellow, and black races, or between the blonde and the brunette. Melanin is a complex substance containing carbon, hydrogen, oxygen, nitrogen, sulphur, and a slight trace of iron. It occurs along with a very resistant unpigmented protein, and its

raw materials are furnished by the blood, and probably from tyrosin and related substances.

In albinos there is obviously an absence of pigment-formation; and this seems to be due to the loss of an hereditary "factor" concerned in the production of the pigment. The pink eyes of true albinos, familiar in white rats and white rabbits, are due to the red blood shining through the unpigmented iris that surrounds the pupil. Of all mammals the Cape Golden Mole has the strangest colouring, for it shows a brilliant metallic lustre, varying from golden-bronze to green and violet of different shades. The precise explanation of this display is unknown, but it must depend on the physical structure of the hairs, not on special pigments. It is an iridescence, changing as we move the animal about. Another antiquity of an animal, the rare Marsupial mole or mole-like Marsupial of Australia, has an unusual red colour which fades or disappears in museum specimens. As to the green colour of the shaggy hair of the tree-sloths of South and Central America, it is entirely an external addition, being due to the presence of minute green algæ, similar to those that paint the trunks of trees in damp situations. They possibly help to make the sloth almost invisible; but it is more probably a very fortuitous association.

Hrdlicka has made an elaborate study of the colour of the hair in "Old Americans", that is to say those who have not been mixed up during the last three generations with recent immigrants; and uses the following classification. He distinguishes, to begin with, emphatically "black", decidedly "light", and unmistakably "red". That leaves between "blacks" and "lights" three intermediate grades—namely, light brown (not blond), medium brown, and dark brown. A noteworthy fact, familiar to all, is that the colour of the hair, unless it be very dark, changes with age. The flaxen-haired baby becomes a brown-locked boy, and he in turn may become dark, though never black. This means a progressive increase in the production of melanin (until grey hairs begin), but why this should come about no one knows. Another general fact is that in Great Britain and in North America there is a greater proportion of dark shades among women than among men—perhaps an illustration of the general proposition that females are more conservative of ancestral conditions. Early Palæolithic man, who used only rough stone implements, is believed to have had reddish-brown to black hair.

The appearance of grey hairs before old age is very common, but in very diverse degrees. The tendency is slightly greater among men than among women. Greyness may mean that in a fresh growth of hair there has been little or no deposition of pigment. Or, as Metchnikoff has shown, an individual hair may turn white because wandering amœboid cells ("chromophages") engulf pigment-

granules in the hair, and carry them off into the skin. Moreover, the replacement of pigment-granules by gas-vacuoles makes the hair white, just as foam is white. In very trying circumstances, a man's hair may turn white very quickly; thus Hrdlicka cites at first hand the case of Greely, the Arctic explorer, whose dark-brown hair became completely white in the course of some months, probably because of the conditions of semi-starvation and great anxiety. Within a year after the explorer's return to civilisation his hair had darkened again, though it never returned entirely to its original chestnut colour. The sudden blanching of Marie Antoinette's hair is believed to be a historical fact; and there are well-documented cases of a man's hair turning white in a single night. One can hardly suppose that this was due to the activity of wandering chromophages; and it is interesting to find that in a case investigated by the physiologist Landois, the pigment was found to be still present, but masked by a profuse production of gas-vacuoles both in the core and the cortex of the hairs.

It often seems as if the colour of the offspring's hair was a blend of the colours of the two parents; in other cases the children seem all to favour one side of the house. The facts remain inadequately known; but the probability is that the matter is much more complex than it appears at first sight, as is true in the case of skin colour in mulattos. It is very likely that what we slump under the title "melanin" is a complex of related chemical substances; and we know that a complex coloration, like that of a wild rabbit, may be controlled by several distinct hereditary factors. We get a glimpse of the subtlety of these matters when we find the handing-on through several generations of a triviality like a white forelock, or a particular "crinkliness" in the hair.

PHAGOCYTOSIS

One of the most common risks of life—or, we may often say, chances of death—is that of the invasion of the body by microbes, which are in some way or other *disintegrative* of its healthy unity. Many diseases—like cholera, dysentery, plague, and tuberculosis—are due to such invasions by specific bacteria; while others, such as malaria and sleeping sickness, are due to microscopic Protozoa, not less virulent. They tend to multiply with inconceivable rapidity within the body, for the division of one, even at the hourly rate (often exceeded), would give over sixteen millions in twenty-four hours. So it is no wonder that with such predatory intensity of growth, necessarily accompanied by corresponding formation of waste-products profoundly deranging the life of their victim, they should bring about disease or destruction. In some cases the activity

of the invaders is strictly localised, and they dissolve away cellular material at a particular spot till a breakage or lesion results, as may be illustrated by the bursting of a superficial sore. Sometimes they multiply so quickly that they block a passage, as the bacteria of diphtheria do—and till lately had to be left to do—in the child's windpipe. Sometimes they produce a toxic secretion which has a poisoning effect far and wide throughout the body. In yet other cases there is both a local and a general disturbance.

But the most important fact is that bacteria produce poisonous secretions which bring about a fatal disturbance in the colloidal proteins of the living cells. There is nothing so disturbing to the equilibrium of a cell (or of the blood) as the introduction of a strange protein; it produces what is often called a "protein shock". As we eat a great variety of proteins, it might be thought for a moment that we should be always having protein-shocks, but this is avoided by the breaking up of the proteins into amino-acids in the process of digestion. Hence, taken internally, even snake venom is digested like white of egg, and is no more poisonous.

Virulent bacteria are rarely, if ever, able to enter an animal through the skin, unless there is some crack or bruise; but a very common mode of infection is when an insect or a tick makes a puncture. In such cases there may be an introduction of a specific parasite, as when the mosquito introduces the malaria Protozoon, or the tsetse-fly the sleeping sickness Protozoon, or the rat-flea the bacillus of the plague. In other cases, where the insect is not known to be the habitual carrier of any specific parasite, there may be an introduction of a casual micro-organism which happens to have found lodgment about the insect's mouth-parts or sting. Thus many people have suffered from blood-poisoning after being stung by the relatively harmless wasp.

There are some interesting external protections, as in the case of young lampreys, where the mucus secreted on the skin has a strong bactericidal effect. But apart from infection through lesions and punctures, there is not much likelihood of intruders getting in through the outer walls of the body.

The first great battle-ground is in the food-canal, where some microbes are able to multiply—in spite of the digestive juices—with sinister rapidity. But the conflict becomes still more serious when the intruders get past the ramparts of the body, and even beyond its (still outer) digestive moat. There comes to be fighting in the canals of the circulation, and even within the inmost homes of life; and as the invaders are on the increase during the battle it often goes hard with the organism. Hence the importance of the "internal defences", among which a first place must be given to the activity of the *phagocytes*.

In all many-celled animals, from sponges to man, with the excep-

tion of Nematode worms and Lancelets (Amphioxus), there are wandering amœboid cells which are able to migrate from place to place within the body. Like Amœbæ they are able to engulf smaller organisms and particles, and in some cases to digest them. These are the phagocytes, or devouring cells. They often occur in large numbers, and may be regarded in fact as *mobile tissue.* In Vertebrates they are specialised white blood corpuscles (leucocytes), but they are able to pass through the walls of the capillaries and to move among the other cells of the body. Yet they are of older origin than the blood, for they occur in animals like sponges and jelly-fishes which have not attained to a blood-vascular system. They may be thought of as body-cells which have retained the mobility and plasticity of Amœbæ.

In 1862 Haeckel observed that grains of indigo injected into a mollusc were soon taken in by amœboid "colourless corpuscles". The hint supplied by this suggestive fact was followed by others; but it is to the credit of Metchnikoff that he recognised the important rôle of these cells as not merely engulfing irritant particles, but destroying them when digestible, thus waging war against intruding microbes and parasite-germs. In his *Lectures on the Comparative Pathology of Inflammation* (trans. London, 1893) he traced through the animal kingdom the devouring function of the wandering cells to which he had given the name of phagocytes. This highly important conception we must therefore outline with special emphasis on the internal defence of the animal body.

The simplest conditions are seen in the Protozoa, for there the whole organism may act as a phagocyte, engulfing and digesting microbes. This is particularly true of the more or less Amœboid Protozoa—the Rhizopods. The experiment has been made of introducing virulent bacteria into a drop of water containing amœbæ, with the result that many of them were ingested and destroyed. In certain cases the bacteria or microbes are actually avoided; for some Protozoa exhibit a sensitiveness (chemotaxis) to particles with which they are not in actual contact. Thus a Myxomycete will creep towards a drop of decoction of dead leaves and away from one of a salt solution; it will "prefer" a nutritive fluid which is not swarming with bacteria to one that is foul with them. It may be here noted in passing that many Protozoa are quick to repair injuries and to regrow lost parts, two processes in which, in Metazoa, the wandering phagocytes often take a constructive share. But the most important point is simply that the phagocytes which form part of the body of a Metazoan are cells that retain the activities of Amœbæ, and not only as regards locomotion, but in their ingestive and digestive powers as well.

In Sponges there is often an avoidance of biggish intruders by the simple expedient of closing the larger pores or oscula—an

interesting process in itself, since it is due to the contraction of spindle-shaped smooth muscle-cells which form a sphincter round the orifice. As there are no specialised nerve-cells, these contractile cells must be neuro-muscular, i.e. "receptors" as well as "effectors". But if a microbe or an irritant particle finds entrance to the interior of a sponge, it is captured by the flagellate cells lining the canal system; and it may be thence passed on to mobile phagocytic cells in the mesoglœa. By feeding sponges with recognisable material, such as carmine particles or milk, then killing and sectioning them at different intervals of time, it has been possible to determine various stages in the capture and transport—from canal cells to the phagocytes, and from one part of the median sponge-tissue (mesoglœa) to another.

In Hydra, where there is practically no mesoglœa, but simply a two-layered arrangement of ectoderm and endoderm, the flagellate and amœboid cells lining the food-cavity act not only as food-capturers, but as "stationary phagocytes". More definitely than in Sponges, the two functions of intracellular digestion and phagocytosis are combined.

In higher Cœlenterates the food-capturing and digesting functions are discharged, as in Hydra, by the endoderm cells lining the food-canal, but most of them have what sponges have, and Hydra has not, wandering amœboid cells in the mesoglœa, which deal with intruded microbes, small parasites, and irritant particles. The same is true of simple worms, such as Turbellarians.

In higher worms and in Echinoderms, the phagocytic cells are usually situated on the peritoneal epithelium lining the body-cavity or cœlom, or else they float in the perivisceral fluid, perhaps also in the blood. They may have several functions, respiratory and excretory for instance, but the phagocytic function is of great importance, all the greater because the cells lining the food-canal have now lost the Hydra's power of *intra-cellular* digestion. That is to say, they do not engulf solid particles as such, to be digested in their interior; they are only able to absorb the fluid into which the food has been changed by the action of the digestive ferments.

Crustaceans, insects, molluscs and the like have a more or less well-developed blood-vascular system, and there are often colourless amœboid cells in the blood like the leucocytes of most Vertebrates. But the phagocytic function still depends, largely at least, on wandering amœboid cells in the body-cavity fluid or in the mesodermic tissues. Yet again, as the vascular system in Arthropods and Molluscs is usually in part lacunar, that is in ill-defined spaces, no rigid distinction can be drawn between phagocytes in the blood and phagocytes in the body-cavity. No case is known, however, in which the leucocytes of an Invertebrate exhibit the power of migrating

through the walls of the blood-vessels to the seat of irritation or injury; in Vertebrates this power is frequently illustrated.

As the circulatory system becomes gradually more highly developed among Vertebrate or Chordate animals, from Tunicates onwards, the number of extra-vascular phagocytes is reduced, and more and more work devolves on those of the blood. In the fin of a young newt an injury or an infection may be dealt with solely by the migratory phagocytes of the connective tissue; in the more frequently observed case—the tail of a tadpole in which blood-vessels have been developed—the extra-vascular phagocytes are greatly aided by leucocytes, which work their way through the walls of the vessels, or are liberated, it may be, by a lesion; in a third set of cases the whole process of defence or repair depends on the leucocytes. It is important also to notice that the endothelial cells lining the blood-vessels may by their contractility assist in the passage of the leucocytes. Sometimes, moreover, as we shall see later, they may free themselves from the wall of the vessel to deal more effectively with bacteria that have been introduced into the blood.

Metchnikoff's particular service was to show that most animals have this bodyguard of free amœboid cells or phagocytes, which are useful in many ways. (1) They are sensitive to bacteria and other intruders, and move towards them; they engulf and digest them. They often crowd together in a clump, and this may lead to a walling in of the microbes which prevents their spreading. It was believed for a time that the phagocytes produced "opsonins", which make the bacteria more susceptible to the attack; but this hypothesis has given place to the view that ("adsorptive") changes in surface tension affect the intruding bacteria, rendering them less resistant. Adsorption means the decrease of free energy at the surface between a solution and a body. The "opsonic index" of the blood is simply the varying degree in which it affects the surface of bacteria that have found their way in and are multiplying.

It is not to be supposed that the bacteria always retreat when the phagocytes appear on the scene. On the contrary, some of them secrete products which keep the phagocytes at a distance; others are able to envelop themselves in a protective capsule; and others, unfortunately, are able to ferment the phagocyte that has engulfed them.

(2) Phagocytes also play a part in transporting material, both nutritive and otherwise, from one area of the body to another. According to Metchnikoff, the occasional *rapid* blanching of hair or feathers is due to the activity of phagocytes, which transport granules of the dark pigment (melanin) from the hair or feather into the skin.

(3) In the healing of wounds and in the replacement of lost parts, such as occurs at the cut end of a worm, there is often phagocytic

activity. But it is obviously difficult to distinguish the members of the normal bodyguard of phagocytes from cells that have arisen through multiplication in persistently embryonic tissue.

(4) Phagocytes frequently help in those drastic changes of bodily architecture which are called metamorphoses. Thus they are active, like microscopic sappers and miners, when the tadpole is changing into a small frog. From the dwindling tail, which is in part dissolved and in part disintegrated, they carry useful material forwards where it may be used in reconstruction.

Metchnikoff distinguished two kinds of phagocytes—(*a*) the microphages, which devour small bodies like bacteria, and (*b*) the macrophages, which devour dead or dying cells, such as exhausted red blood corpuscles, or transport granules, as we have mentioned in connection with rapid whitening of hairs or feathers. He gives a vivid account of the invasion of the brain of a very long-lived parrot by macrophages which proceeded to do away with exhausted nerve-cells. His general thesis as regards inflammatory processes in the body may be stated in his own words: "Inflammation generally must be regarded as a phagocytic reaction on the part of the organism against irritants—a reaction carried on by the mobile phagocytes." In the strict sense inflammation is not a diseased state; it is the clash and struggle between the organism's bodyguard and intruding microbes or irritants.

THE RETICULO-ENDOTHELIAL SYSTEM.—We have seen then that Metchnikoff disclosed more especially the rôle of the migrant phagocytic (microbe-devouring) cells which serve as one of the chief internal defences of the body. They form a mobile bodyguard not merely brought where needed by the blood stream, but able like amœbæ to move independently by pseudopods. But besides this mobilised force there are Metchnikoff's more or less stationary "macrophages", which are definitely located—like garrisons—in various tissues of the body. After long neglect they have come into prominence again and been much studied of recent years, e.g. by Aschoff and his pupils. They are generally referred to as the *reticulo-endothelial system.*

They are notably to be found in the spleen, the liver (there called Kupffer's "stellate cells"), and the bone marrow. They also occur as "histiocytes" scattered through the connective tissue, which forms, as it were, the girder system of the body, especially when it is solidified into cartilage or gristle, or reinforced by the deposit of lime-salts to form bone. These histiocytes appear to be persistently embryonic cells, for two types of them give rise to two kinds of phagocytes that occur in the blood of higher Vertebrates. They are also allied to the red blood corpuscles.

Now all the cells of the reticulo-endothelial system possess the

power of capturing solid particles, phagocytosis in short; and they also show to a greater or less degree some power of independent movement. They play a great part in the reactions of the body to certain infections. They are, in early stages, the destroyers of the bacilli of tuberculosis, and in later stages the chief victims of these insidious intruders. They also come to form part of the tubercle itself, that is to say the scar-tissue that becomes a firm nodule enclosing the badly damaged tissue. They have a significant relation to the virus of certain cancers, as Dr. Gye and Mr. Barnard have shown; and, if transplanted from one animal to another, they may start the disease afresh. In local inflammations they act as scavengers, and, on the other hand, they may in such cases help in the formation of new tissue, replacing what has been destroyed.

In conditions of health, the histiocytes play a great part in the destruction of red blood corpuscles which is always going on, for these important cells have but a short life. It follows from this connection that the activity of the reticulo-endothelial system has something to do with cases of pernicious anæmia, where a normal balance of repair and waste is disturbed by a destructiveness that runs riot. Lastly, it is becoming clear that the histiocytes are intimately associated with another of the body's internal defences, namely, the production of "anti-bodies", which demand a paragraph to themselves.

ANTI-BODIES OR ANTI-TOXINS.—This is a convenient term for specific chemical substances which serve to neutralise specific poisons or toxins. They might also be called *counteractives*. Roux and Yersin discovered the toxins of microbes; Behring and Yersin demonstrated the reality of anti-toxins; Roux and Martin showed how specific anti-toxins might be produced by introducing a specific microbe into the blood of some animal, such as the horse, and then used for injection into man (or some domesticated animal) in anticipation of, or even subsequent to, an infection with the virulent microbe in question. Lest man's native powers of producing anti-toxin for himself should be inadequate as regards the amount produced or as regards rapidity of production, he may receive extraneous assistance. The value of the injected anti-toxin that works against the rapidly poisonous secretion of the diphtheria microbe is attested by the number of children whose life it has saved. Even against snake-poison, which is non-microbic, an extraneous anti-toxin may be successful. Snake-poisons are proteins, and it is against strange proteins, such as those secreted by virulent bacteria that anti-toxins work.

It should be noted here that no one has as yet succeeded in isolating an anti-toxin; what is injected is a serum-preparation, including the anti-toxin. It is not indeed certain that anti-toxins are definite

chemical entities, for they may be properties of the colloidal equilibrium of the blood and its cells. Their effect may be physico-chemical rather than chemical. But no one doubts their *reality*.

THE BACTERIOPHAGES.—This unfamiliar word refers to an interesting discovery made by Dr. D'Herelle, of the Pasteur Institute,—a discovery (1918) which stands for something new, even if it does not turn out as the investigator expected. Bacteriophage means bacterium-devourer, and D'Herelle's theory is that we have normal partners which destroy some of the bacteria that invade our bodies. A bacteriophage is a living organism of extreme minuteness, far smaller than an average bacterium—a life-size diagram of which may be seen with a good lens inside the second "o" of the word good. The particular species which D'Herelle discovered in 1918 is called *Bacterium intestinale*, and this tells us where it lives. Some fierce critics say that its name should be "mare's-nest", but that is not fair to D'Herelle, who has certainly discovered a *phenomenon*, whether his interpretation be right or wrong.

What is D'Herelle's phenomenon? If a few bacteria of the pyocyanic species be added to a culture of dysentery bacteria they multiply and produce ferment-like secretions dissolving the virulent bacteria amongst which they have been introduced. But D'Herelle found that when a clear filtrate is made of some of the debris from the food-canal of a convalescent dysenteric patient (a filtrate that is quite limpid and passes through a porcelain filter), it has a rapid solvent effect when introduced among the dysentery microbes. It can be multiplied indefinitely; its power is not lessened by dilution; it behaves as if it contained microbes. In carefully controlled conditions it will form spots on a gelatine plate, and if a platinum thread be drawn through one of these spots and then placed in a culture of dysenteric bacteria the result is a rapid solution of the latter. In indirect ways it has been found possible to estimate the size of the invisible corpuscles that D'Herelle regards as Bacteriophages. They are ten times smaller than the smallest bacterium visible under the microscope; but they are several times larger than the invisible germs of the ultra-virus diseases, such as foot-and-mooth disease.

Perhaps D'Herelle's phenomenon is due to something like an anti-toxin, which is almost like an "x". But it seems impossible at present to prove that he is wrong in ascribing it to the agency of a living organism (his *Bacteriophagum intestinale*) which is part of man's normal bodyguard. His picture is an interpretation of facts. It leads us to think of extremely minute and very useful symbions, living in our food-canal, producing a secretion of high opsonic potency, which educates the phagocytes and prepares injurious bacteria for death. Organisata non sunt multiplicanda præter

necessitatem; but if D'Herelle has not discovered an organism, he has certainly discovered a remarkable fact.

We must now return to an allied puzzle of great biological interest—immunity.

IMMUNITY.—It is a well-known fact of Natural History that a hedgehog may be bitten by an adder without suffering any evil effects so far as can be seen. This has been corroborated experimentally, and it appears that a hedgehog does not suffer from an injection of poison many times stronger than the fatal dose for a rabbit. The hedgehog has natural immunity to the venom of vipers.

But what does this immunity mean? The first step towards an answer is not difficult, and has been well worked out in connection with the attractive carnivores known as the Ichneumon (*Herpestes ichneumon*) and the Mongoose (*Herpestes mungos*), both of which are inveterate enemies of snakes, and enjoy the same natural immunity as the hedgehog. If some cobra's poison be mixed with mongoose's blood, and if the fluid or serum be injected under a rabbit's skin, nothing happens; but an injection of the same amount of poison without mongoose's serum is immediately fatal. The same is true for the hedgehog and adder's poison. Evidently, then, there is some substance or quality naturally present in the blood of mongoose and hedgehog, which is able to counteract, neutralise, or somehow take the edge off snake toxins.

The point may be made clearer by taking the case of the pig, which is not affected by the bite of several different kinds of venomous snake, or by subcutaneous injection of prepared snake toxin. The pig is not affected, for instance, by cobra poison; yet if the blood-fluid or serum of an uninjured pig be mixed with cobra poison and then injected into a rabbit, there is an immediately fatal result. This obviously suggests that the pig's blood does *not* contain any "anti-toxin" that can neutralise snake toxin. What makes the difference? It is believed that the pig's "immunity" is more apparent than real, that it is due to the protection afforded by the thick layer of fat below the skin. This familiar fat includes very few blood-vessels, and it probably serves to stop the poison from getting further in.

The hedgehog, the Ichneumon, and the mongoose can withstand large injections of poison; thus the Ichneumon can successfully counteract six times the dose that is fatal to a rabbit; but in all cases there is, naturally enough, a limit beyond which the poison is lethal. A few other mammals are known to be immune to snake poison; thus the American opossum is not affected by the bite of a rattlesnake, and the cat has a high degree of immunity to the poison of vipers of various kinds. A few mammals have a distinct but slight insusceptibility to snake poison; most have none at all.

The cobra's poison has no effect on other cobras of the same species, and this is a general rule. But when a venomous snake bites a relative that belongs to a different species, the result may be fatal, as is generally the case with different kinds of vipers. A cobra is not much affected by a viper's poison, while all vipers readily succumb to a cobra's. All this shows how *specific* the immunity may be. There are many peculiarities of this sort which do not readily find explanation at present. Thus if the blood of a crayfish be injected into a mouse, it confers immunity against the poison of a scorpion! Yet the crayfish itself is far more sensitive than the mouse to scorpion poison.

ARTIFICIAL IMMUNITY.—The immunity which is so well illustrated by the hedgehog to adder toxin and by the mongoose to cobra toxin is *natural* immunity; but the same quality of insusceptibility may be more or less artificially *acquired*. One method is to begin by injecting minute doses of the poison, and to continue with gradually increased doses. The other method is to inject a serum preparation of the blood of an animal that has been immunised by graduated direct doses of the poison, or by non-fatal attacks of the virulent microbes. Some animal, such as a horse, is rendered immune, and its serum, abounding in anti-toxins according to the theory, is injected into another organism. This method is less drastic than the other, yet very effective.

Another form of immunity is very familiar, namely that which follows recovery from a disease. The individual is more or less protected against taking the disease a second time. The immunity may last for many years in the case of smallpox, but there are records of two or even three attacks; it may be strong, as in the case of scarlet fever, measles and mumps; it may be transient, as in diphtheria. There are rare cases, such as pneumonia, where the immunity is at most very temporary; where indeed susceptibility to the disease appears to be increased, not decreased.

There is evidence in some instances that an artificially immunised rabbit or guinea-pig has young ones which are born immune. The same is asserted in regard to smallpox, that the immunised human mother may confer immunity on her offspring; but it is difficult to prove this satisfactorily. If it occurs, it may be due to specific anti-toxins passing through the placenta from the blood of the mother into that of the unborn child.

When there is evidence of immunity as a racial character, as in the case of negroes, who are relatively immune to yellow fever and malaria, or in the case of Algerian sheep, which are relatively immune to splenic fever or anthrax, the explanation is probably that a constitutional variation, like the hedgehog's, arising apart from infection or other poisoning, has become hereditary, whereas those

members of the race who did not vary in the direction of immunity would be gradually eliminated.

CLASSIFICATION OF POISONS.—No hard-and-fast line can be drawn between poisons and other substances. For there are many chemically diverse kinds of poisons, and even if we say that a poison is defined by its destructive or disintegrative effect when introduced into a living creature, we have to admit that one man's food may be another man's poison, and that much depends on the dose. Common salt is necessary for health, but an enormous dose would be fatal. Sugar also may be a poison. Many a powerful poison, such as strychnine, may be life-saving in a minute dose. An adder's venom will kill a rabbit, but the hedgehog is unaffected. The ovaries of the sea-urchin are often eaten along the Mediterranean coasts, but they produce symptoms of poisoning if used just before they are about to discharge the eggs. There are strange stories of ducks being poisoned by swallowing ripe earthworms.

The poisoning effect has two sides; it often varies with the physiological state of the assailant or poisoning animal, and also with the condition of the victim or poisoned animal. It may vary with the moon. A strawberry is poisonous to some people, and lobster to others. The hornbill enjoys the seeds of nux vomica; and while swallowing one blister-beetle would probably be fatal to a man, the scorpions suck their juices with impunity.

All living matter, as we have explained, is made up of the nitrogenous carbon compounds called proteins, such as the albumin of white of egg, or the casein of milk; yet each distinct type of animal has specific proteins peculiar to itself. And these proteins, for some reason or other, are not good mixers. If the serum of the blood of a particular animal is introduced into the blood of another animal, even a related species, it brings about a destruction of red blood corpuscles. The strange protein has a disintegrative influence, even on substances not very unlike itself. In other words, the strange protein acts as a poison.

But as man is continually using various proteins as food, and experimenting with proteins that he never tried before, we have to recognise the value of those digestive processes that break down the proteins into their constituents called amino-acids. The smaller molecules that result from the breaking-down of larger ones are able to pass more readily through the wall of the food-canal into the absorbing blood-vessels, and that is great gain; but another aspect of the process is that the edge is taken off the strange proteins. They are disarmed, as it were; more precisely, they become harmless by being broken up into their constituent amino-acids. Thus we can understand how man can profitably eat many substances which would kill him if introduced into his blood. Not that the blood gives

in to poisoning without making a struggle! Indeed, it may react so effectively, by producing counteractives or anti-toxins, that the animal becomes immune.

In his recently published *Gifttiere* (1927), Prof. E. N. Pawlowsky of Leningrad has given an interesting grouping. First of all, there may be separated off those animals that have no special poisonous organs or glands, yet may prove their virulence if they are used as food, or if their blood, extracts, or exudations are introduced experimentally or non-aggressively into some other creature. This is a passive poisonousness, depending on some peculiarity in the chemical composition of the poisoner's tissues. It is well illustrated by most of the inflatable "Puffers" or "Globe-fishes", by the "Blister-beetles", whose blood is rich in the poison cantharidin, and by a number of parasites, such as threadworms, whose exudations have a poisoning effect.

All the other poisonous animals, extraordinarily diverse in nature, have this in common, that they have specialised structures or organs for the preparation of the poison and its aggressive expulsion into or on to a victim. Thus, to begin near the base of the genealogical tree, there are the jelly-fishes and sea-anemones and Portuguese Men-of-War, whose epidermis contains myriads of stinging-cells. The ejection of microscopic lassoes liberates poisons, such as thalassin and congestin, which are often very virulent, as bathers sometimes discover. Besides discouraging the attacks of hostile animals, the stinging threads often serve to paralyse and capture the small organisms that are used as food.

Another group may be defined to include a large number of insects that exude irritant blood aggressively from various strategic points on their body. The expulsion is sometimes a gentle exudation, as in oil-beetles; but it may be energetic enough to deserve the name of squirting, as in the large caterpillar-like larvæ of the birch saw-fly. There is an Algerian Locustid that squirts out a double jet of orange-coloured blood to a distance of two inches! This is very striking, yet it is also puzzling. For one cannot help thinking that blood is much too precious to be utilised in this reckless way. Perhaps the expulsion relieves blood-pressure; perhaps it does not happen very often.

The most highly evolved animal-poisoners are those that possess, not only poison glands, but some specialised arrangement for introducing the venom into a victim. Perhaps it might be useful to condone and even adopt the peculiar use of the word "sting" to denote any of these poisoning instruments, which are so diverse in nature. The spider "stings" with its first pair of mouth-appendages, the scorpion with a sharp spine at the end of its tail; the duckmole stings with a spur, the weaver-fish with a fin-ray; the procession caterpillars and many others sting with their nettle-like hairs. How

striking it is that a venomous snake should have evolved its poison-injection apparatus out of the tooth, while a bee's sting is a transformed egg-laying organ!

In conclusion: Our human conception of the poisoner is emphatically sinister, but among animals the use of poison is as often protective as aggressive.

WHAT IS LIFE?

(1) Modern discussions of the perennial question: What is Life? have shown in varying degrees a recognition of the commonplace that hopeful progress towards an answer lies in *a fuller knowledge of living creatures*. No amount of verbal dexterity or even profound reflection over the concept of "life" floating in detachment will much advance understanding, unless we are at the same time deepening our acquaintance with organisms, from microbes to men, and trying to see life whole, not as a biochemical witch-pot merely, but as the activity of individualities that develop, grow, and reproduce, that struggle, vary, and evolve. If we are to answer the question: What is Man? or What is Personality? we must deepen our knowledge of men and of personalities, and of Shakespeare and Newton as well as of Bushmen. So to avoid false simplicity in our answer to the question: What is Life? we must seek a comprehensive, all-round, and intimate view of organisms, taking account of intelligent apes as well as of dimly purposive Amœbæ, and of psychobiosis as well as of biopsychosis. We cannot make sense of any kind of life without recognising the importance of fermentation, but we cannot make sense of the life of higher animals apart from feeling, intelligence, and some sort of purpose; and the continuity of organisms makes it probable that the dim analogues of these psychical qualities are present throughout.

The extreme behaviourists or biomechanists will, of course, refuse to take account of any process that does not admit of physico-chemical analysis and description, but this position does not work out well in our daily life and conversation, where we have to allow at every turn for intelligent or even rational purpose. Yet even these extremists will agree with our *first* proposition that a better understanding of life is likely to follow a deepening and widening of our study of organisms.

(2) It seems to us that no one has as yet succeeded in re-describing in terms of anything else a fair and intact sample of that distinctive kind of activity that we call life; and it is *possible* that the nature of life lies outside the realm of the knowable. But even if we cannot understand what *life* essentially is, it is surely useful to return to the bed-rock of facts and seek to envisage *living*. This is our *second* proposition. The fundamental fact is that living creatures act on

their surroundings and are acted on by them. Taking the first letters of the three biological co-ordinates—organism, function, and environment—we suggest as a descriptive definition of living: $O \rightarrow f \rightarrow e$; $E \rightarrow f \rightarrow o$. In condensed formulation living is an ever-changing ratio between O, f, e and E, f, o, or O, f, e/E, f, o, the numerator aspect being prominent at one time, the denominator aspect at another. This is obviously no definition of "life", since the words organism and function imply the whole mystery; yet it is a very useful positivistic conception; and it may save us from the fallacy, still frequently illustrated, of trying to define organism apart from environment, which is absurd. Whatever be the true inwardness of life, the facts that we study are: $O \rightarrow f \rightarrow e$; $E \rightarrow f \rightarrow o$; $O \rightarrow f \rightarrow e$, and so on in succession.

(3) It is always useful to get below superficial differences to fundamental resemblances. Thus it was a notable step when Huxley united birds and reptiles as Sauropsida, and a still greater when Claude Bernard justified Linné's term Organisata, by showing in detail the phenomena common to the life of plants and animals. On the other hand, there is danger in satisfying our desire for unity, or for continuity, by sticking the same label on things or processes which remain very different. Thus, as we have shown in another section, the word "evolution" is used as a label for a variety of genetic processes which have not very much in common save that they are all *modes of becoming*.

There is a tendency to do the same with the word "life" or "organism". It is generally admitted that Herbert Spencer did more harm than good with his term "social organism", and Whitehead has made something of the like exaggeration, in the opposite direction, in his emphasis on the organism-like character of the atom. So our *third* proposition is that, when all is said, the orders of fact indicated for short by the terms "matter", "life", and "mind" remain very different from one another. Perhaps it would be clearer, in spite of the pedantic words, to say that "cosmosphere", "biosphere", and "sociosphere" are three different worlds, one within the other, each with its own distinctive concepts, categories, or descriptive formulæ. No one stands for continuity more firmly than General Smuts, yet he insists that "matter", "life", and "mind" are to be regarded as three quite distinct orders of fact. This does not mean that they are separated by hard-and-fast boundaries, for it is certain that organisms are whirlpools of matter and energy; that the members of a human society are rational mammals; that mind is clearly emergent in many an animal. If anything is gained, something is lost by speaking, as some distinguished thinkers do, of "the life of crystals", or "the organism of the atom", or "the fellowship of molecules", or "the society of cells" in the body. Organism, for example, is a clear-cut, well-established term; and it

should be kept for genuine organisms, not blunted by application to atoms on the one hand, or to human societies on the other.

Thus our third proposition is that the domain of things, the realm of organisms, and the kingdom of man (where mind plays a dominant part) are three distinct orders of fact, each with its characteristics—distinct though they overflow and interpenetrate, distinct though their continuity is becoming increasingly clear.

(4) It is a waste of time and wits to continue to pit against one another the mechanistic and the vitalistic descriptions of living creatures, as if one must choose between them. Every reasonable vitalist, whatever school of vitalism he represents, wishes good speed to chemicophysical analysis and description; but his protest is that the sea of reality contains fishes which must escape the physicochemical nets. The physicochemical meshes or methods are not adapted or intended to capture them. There is no chemical test for feeling; there is no balance that will weigh a purpose. Yet the vitalist believes in the *reality* of feeling and purpose; and is rather amazed that anyone can disagree with him. Every vitalist wishes to see biochemical and biophysical analysis pushed as far as they will go—they express, in Comtian phraseology, "legitimate materialisms". But care must be taken not to pretend that the biochemical and biophysical concepts must suffice, or do suffice, for the description of the whole of life or living. It is also more than a little naïve to suppose that atoms and radiations and the like form a sort of bedrock of reality, the fact being that they are only certain aspects of reality which become clear when certain methods are used in certain fields. And their mirroring, increasingly cleared from blurs, is *ours*.

Similarly, in the opposite direction, there are "legitimate transcendentalisms", as when we insist on including feeling and the like in our account of animals; or when we consider the possibility that something analogous to the mental aspect of an intelligent animal may be at work in the implicit organism which we call the developing ovum. General Smuts suggests (in his *Holism*) that mechanism and vitalism should both be discarded as mischievous survivals, but that is impossible. They represent two legitimate ways of looking at living creatures. It is true, however, that they require to be replaced by neomechanism, and neovitalism, for the mechanistic formulations of to-day are not those of fifty years ago, and vitalism has also been changed by a deepening knowledge of the non-living and of the unconscious. Our *fourth* proposition is that mechanistic and vitalistic descriptions are not only legitimate, but even necessary for clearness.

(5) The extreme mechanistic position is not that there is a chemistry and a physics of the living organism, for that is admitted by all; it is that the concepts of chemistry and physics suffice to

cover the whole field of life. When Dr. J. S. Haldane punctures a would-be entirely mechanical description of the work of the kidneys or the lungs; or when Smuts points out that many of the reactions of organisms differ from those of non-living systems in being the unified responses of co-ordinated wholes of a higher order than, say, atoms or chemical compounds; or when Driesch shows how mechanistic formulæ fail to grip the facts of development, and so on, the mechanists point to what the future may have in store in the way of complete mechanistic description. This is unanswerable, though it may seem optimistic. It remains, however, for the vitalist to point out that in the higher reaches of life the mental aspect is undeniable, and that mentality cannot be juggled out of mechanism. Moreover, to put a long argument briefly, a machine cannot have a theory that it is a machine. Our *fifth* proposition is that mechanistic methods are indispensable and invaluable, but have their dangers just like facile vitalistic ones, and do not lead to adequate descriptions of living.

(6) At the opposite pole is positive vitalism, ably represented, for instance, by Prof. Wildon Carr, who maintains with emphasis that mechanism is not to be *supplemented*, but is to be *rejected* as a wrong way of approaching the problem. Like Driesch, he stands for the postulate of an "entelechy", a positive principle in virtue of which an organism is an individual whole and acts as such. The essence of life is individual and purposive activity, and this is original and of the essence of reality. What we know of matter does not help us to understand life and mind.

But a radical objection to this view is the apparent continuity of evolution. For it looks as if living organisms had emerged (at present one of the "blessed" words) from non-living materials; it looks as if undeniable "minds" or mental aspects had arisen as new syntheses in animals the ancestors of which were not more than latently mental, just as the clever child arises in individual development from an egg-cell, the "mind" of which is hard to seek. But Wildon Carr and many who think with him would definitely reject the evolutionary precedence of matter to life, and of life to mind.

According to General Smuts, who is regarded by Carr as an entelechist without knowing it, evolution has been a progressive emergence of higher and higher "wholes", such as the atom, the cell, the vegetative organism, the animal with an embodied mind, and the human personality. A new "whole" is a fresh synthesis, the intrinsic nature of which admits of new agency, creativeness, and freedom. The progressive emergence of "wholes" in Nature allows of the expression of fresh aspects of reality; and if it be asked why there should be this tendency to whole-making, Smuts replies, if we understand him aright, that such is the nature of things. Man lives

in a "holistic" universe. Within the scientific universe of discourse Smuts refuses to invoke any *deus ex machina*. Yet when he defines holism as "the ultimate synthetic, ordering, organising, regulative activity in the universe which accounts for all the structural groupings and syntheses in it, from the atom and the physicochemical structures, through the cell and organisms, through mind in animals to Personality in man", he is almost laying himself open to Carr's charge of "using a wrong word 'holism' when the right word 'entelechy' was staring him in the face". Yet of the two formulators, we think that Smuts keeps nearer than Wildon Carr to the facts of the case; for holism emphasises continuity and evolution.

(7) Finally, it seems to us that the most tenable position is what may be called "methodological vitalism". Mechanistic descriptions are indispensable, and we owe to the mechanists in particular a deeper understanding of the environmental factor in living (E→f→o). But at its best, at present, mechanistic formulation is far from giving us an adequate account of the life of organisms. Vitalistic descriptions are also indispensable, for whether the organism has an entelechy at heart, or whether it is one of a long series of "syntheses", or "integrates", or "wholes", its life cannot be adequately described in terms of mechanism. The vitalists have done good service in emphasising the organismal factor in living (O → f → e), and also, of course, the functioning factor, for life is *par excellence* activity, as Wildon Carr so well insists. But the scientific inquirer is not fond of "principles" or "entelechies", and he dreads "vital forces" in disguise; so what can he do but maintain, not a positive, but a methodological vitalism? That is to say, as things are at present, the mechanistic formulation of organisms and their functionings in their environments does not answer the distinctively biological questions. Biology has concepts of its own at present irreducible to chemistry and physics: the living creature is an historic being enregistering its experience; it is a purposive individuality that gets things done; it grows, multiplies, develops, struggles, varies, and evolves; it often has a mind of its own.

CHAPTER IV

REPRODUCTION AND SEX

It is difficult to find in the non-living world any analogue to the multiplication of organisms. Even when a complex molecule gives rise to two simpler ones, or a planet liberates a satellite, the resemblance to the division of an Amœba or to the budding of a yeast-plant, is remote. The power of reproducing is one of the criteria of life.

The general term reproduction includes the whole sequence of processes by which new individuals arise. From a parent organism,

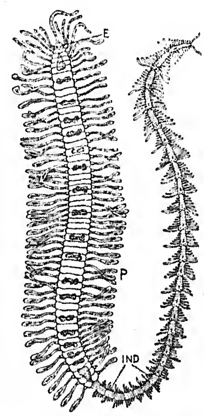


Fig. 54.

A Polychaet Worm (*Myrianida fasciata*). From Malaquin. The anterior body (P) buds off from a posterior zone a chain of numerous individuals or zooids (IND); E, eyes on the head of the original individual.

or more usually from two parents, offspring take origin, often at successive reproductive periods, which implies *multiplication*; these offspring give rise in due time to others, and this implies a *succession of generations*. It is not possible to separate reproduction in any rigid way from growth, at the limit of which it usually occurs; or from the activation of the reproductive organs at maturity, in which, in Vertebrates, hormones are often concerned; or from the division of labour implied in there being two sexes, egg-producing or female individuals and sperm-producing or male individuals; or from the ways in which the sperm-cell is brought into contact and union with the egg-cell—a process in which the insemination, the pollination, and the like must be distinguished from fertilisation proper—

the intimate union of the reproductive units (gametes), to which Weismann applied the useful term Amphimixis. But the process of reproduction has also to take note of early development; and, also, of such antenatal relation as may be between parent and offspring. Nor can the study of reproduction be separated off from that of heredity—that relation of organic continuity between successive generations, which secures the begetting of like by like, and yet allows of the emergence of those novelties or variations which become so significant in further evolution.

MODES OF REPRODUCTION.—In one-celled organisms, whether Protists, Protophytes, or Protozoa, the unit divides by

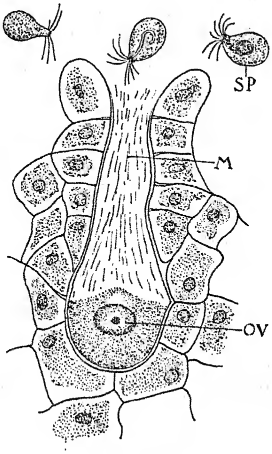


FIG. 55.

The Female Reproductive Organ of the Adder's-tongue Fern (Ophioglossum). After Bruchmann. At the base there is an egg-cell or ovum (OV), and in the entrant canal a secretion of mucilage (M). Some ciliated sperm-cells (SP) are attracted to the entrance, and one of them will normally unite with the ovum and effect fertilisation.

fission, budding, or spore-formation into two or more parts, and each of these parts grows into the likeness of the whole. Yet even at this low level of unicellular life it often happens that two individuals combine to form one. The single product of this total conjugation may rest for a time, but sooner or later proceeds to divide into many. In many higher Protozoa, there arise specialised reproductive units (gametes)—sometimes even dimorphic—and these unite by pairs, forming a "zygote", which either grows into the original form or divides into many individuals. Very suggestive also is the partial conjugation of such ciliated Infusorians as the Slipper Animalcule (Paramœcium), where there is an exchange of nuclear elements and then a separation of the conjugating pair.

This process seems to maintain vigour and to promote variability in the stock. Here experiments have been of interest. In artificially isolated "pure lines" (all descended from one), no conjugation occurs, yet there is a periodic (it may be monthly) occurrence, in many or most individuals, of a remarkable process (endomixis), in which the nuclear organisation is disintegrated and reconstructed. The individuals behave as if they were about to conjugate with one another, but no conjugation occurs. This disintegration and reintegration here suffice to secure continuance of vigour—in fact rejuvenescence.

Among many-celled organisms, both plants and lower animals, there is frequently a completely asexual reproduction, in which an existing part of the parent or a new growth from it is separated off to start a new individual. Thus the freshwater Hydra forms buds, which attain adult form before separation; a sea-anemone may not only bud, but may divide vertically into two; a ribbon-worm (Nemertean) may break into half a dozen pieces; two or three kinds of starfish can normally multiply by separating off their arms; a liverwort may give off multicellular gemmæ and a tiger-lily drops its bulbils. In short, there is great variety of asexual multiplication; and this often leads to the formation of colonies, as in zoophytes and corals, Bryozoa, and compound Tunicates.

But all the many-celled animals and the great majority of many-celled plants show sexual reproduction; though the asexual mode also often occurs in the same organism. Thus while the main mode of multiplication in the freshwater Hydra is the liberation of asexually-produced buds, there is also sexual reproduction by eggs and sperms. Here we have to note: (*a*) the formation and segregation of special reproductive cells, (*b*) the production of the two different kinds of special reproductive cells, and (*c*) the production of these (the ova and spermatozoa) by different (male and female) organs or individuals. In plants like ferns and mosses, one phase in the life-history is the formation of spores—reproductive cells arising apart from gonads and capable of developing without fertilisation. Such cells occur among animals also, as in the life-history of the liver-fluke, where the larvæ multiply by spore-cells, while the adult reproduces as usual by ova and spermatozoa (see Alternation of Generations).

In some animals, such as certain Rotifers, males are not known; and in some other types they are absent for long periods (as in summer greenflies), or seeming unnecessary even when they are present. In other words, Parthenogenesis often occurs; yet this may best be thought of as the unisexual mode of sexual reproduction. For although there is no fertilisation, there is multiplication by means of egg-cells. Many common animals, such as snails, earthworms, and leeches, are hermaphrodite; that is to say,

each organism is both an egg-producer and a sperm-producer; often, it must be noted, at different times, as in the "dichogamy" of so many flowers. In such animals as those above mentioned, there is cross-fertilisation in spite of hermaphroditism; in a few other cases, such as the liver-fluke and some tapeworms, there is self-fertilisation ("autogamy").

ADVANTAGES OF SEXUAL REPRODUCTION.—The biologist must seek to explain the processes which bring about the separation of parts, e.g. the formation of buds, as in Hydra, or the loosening off of part of the body, as in Planaria, and also the multiplication and liberation of eggs and sperms, as in most animals. We shall

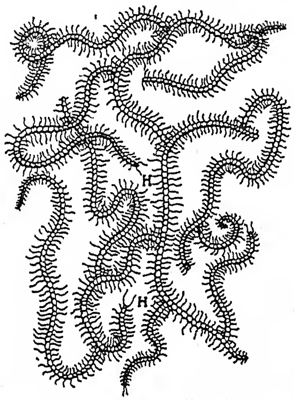


FIG. 56.

Asexually Branching Marine Worm (*Syllis ramosa*). After McIntosh. Two heads (H) are shown, and there is a fusion of branches forming a network.

return to these difficult physiological problems; but we give a prior place to the question: What advantages has sexual reproduction over asexual methods? Most plants and animals exhibit sexual reproduction, though some retain asexual multiplication as well: what justifies the sexual process?

There is an advantage in the fact that a larger number of offspring can be started at once by the sexual method, and this usually with relatively less drain on the resources of the body. That sexual reproduction is fatal to the individual in many cases (e.g. butterflies, eels, etc.) does not disprove the general proposition that sexual multiplication tends to be, and generally is, a more economical mode of reproduction than the asexual process. We use the term "multiplication" as often as possible for all modes of increasing the number of individuals, and correspondingly use the term "reproduction" when there is more or less distinct sexual differentiation.

Although asexual multiplication occurs in some complex animals,

even up to Tunicates, it is attended with obvious difficulties as the creature becomes highly differentiated and integrated. Thus it does not occur in Arthropods or Molluscs, nor in any Vertebrates proper, i.e. above the level of the degenerate Tunicates. The outstanding fact implied in having specialised reproductive units is that they have not contributed to the building up of the parental "body", and thus have retained an organisation continuous in quality with the original germ-cell from which the parent arose. They are thus not very liable to be affected by the mishaps which so frequently befall the "body" which bears them. A separated-off fraction or bud of Hydra, sea-anemone or planarian has been shown to start with

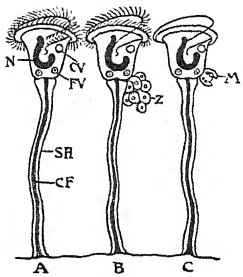


FIG. 57.

The Bell Animalcule, Vorticella, a microscopic Infusorian, often seen as a fringe on waterweed. A, an ordinary individual, showing the stalk with a contractile fibril (CF) inside a non-contractile sheath (SH). The nucleus (N) is horseshoe-shaped. There are cilia around the mouth; CV, a contractile vacuole; FV, food vacuoles. This individual (II) may produce a bud at the lower end of the bell, and this may divide into eight minute zooids (Z). In III a minute zooid, a microzooid (M), is seen entering the ordinary individual. This is comparable, *mutatis mutandis*, to a sperm-cell entering an egg-cell.

disabilities that the parent body may have acquired, through unfavourable surroundings or food—an obviously undesirable handicap.

In the life-history of the germ-cells, and in the mingling of sperm-cell and egg-cell in fertilisation, there is abundant opportunity for new permutations and combinations of hereditary qualities—for variations, in short. Here is surely the crowning advantage of sexual reproduction, that it favours the emergence of the new. Yet perhaps we may look further ahead and recognise that sexual reproduction, in animals especially, leads to separate sexes, often dimorphic, whence courtship, the dawn of the love of mates, and the evolution of parental and other emotions. It must be noted that we are not here forgetting the physiological problems already recognised, nor falling into the teleological fallacy of trying to account for origins by indicating the purposiveness of the new departures. We are merely pointing out the survival values of sexual, as contrasted with asexual, reproduction.

Reproductive and Other Functions.—It is often and rightly said that most of the activities of organisms centre round the contrasted functions of nutrition and reproduction. The activities of the green leaf stand in marked contrast to those of the flower. The zoophyte colony is nutritive and vegetative, the swimming-bells or medusoids that they bud off are reproductive and energetic. The larval Mayfly may have a nutritive sub-aquatic life of two or three years, and a reproductive aërial life of two or three evenings. In the year's life of migratory birds the courting, mating, nesting, and brooding period is sharply punctuated off from the resting and recuperating period spent in the winter-quarters. Life is often a see-saw between Nutrition and Reproduction, using both terms widely.

Yet it is evident that nutrition and reproduction are not neces-

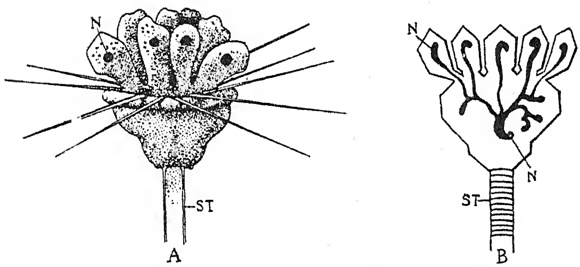


Fig. 58.

Budding in Stalked Infusorian (Ephelota). After Bütschli and Saville Kent. A, the intact animal on its stalk (ST), with a nucleus (N) in each bud. B, a diagram showing the branching of the original nucleus to form the nuclei of the several buds.

sarily to be regarded as two sharply circumscribed functions, for they each imply the direction of numerous activities towards two particular ends: (*a*) the preservation of the individual, and (*b*) the continuance of the race. Thus in studying higher animals it is impossible to consider either reproduction or nutrition apart from the functions of moving and feeling, or apart from the circulation and the hormones. There may be an abstracting fallacy in too sharply punctuating off the reproductive function, which means much more than the activity of the reproductive organs or gonads. Many other functions may be ancillary to reproduction, which, moreover, in the higher reaches of life, has its psychological as well as its physiological aspect. The point is that reproduction and nutrition in their more complicated expressions must be regarded as co-ordinations of several functions towards a particular end or satisfaction. The quest for food and the search for mates may be orchestrations of many functions.

NUTRITION AND REPRODUCTION CONTRASTED.—With the preceding saving-clause in view, it is now important to lay emphasis on the contrast between nutrition and reproduction, which is indeed one of the fundamental ideas in biology. Nutrition not only implies fuel for immediate consumption, it implies an increase in the capital of the body, either in the form of stored reserves, or as a fresh growth of tissue. *It has emphatically a plus sign, whereas reproduction is always minus.* For reproduction always means parting with some of the living material. The simplest expression of reproduction is seen when a single-celled organism divides into two; but even in this case the unit must be said to give off half of itself. In an animal like a fish there is an enormous reproductive sacrifice or expenditure, for many hundreds of thousands of egg-cells and still larger numbers of sperm-cells are set adrift into the water. It has been estimated by Mortensen that one of the starfishes, *Luidia ciliaris*, may liberate two hundred millions of egg-cells in a year. It is not surprising that the reproduction of many types is followed by the death of the individual, as is illustrated from the delicate Mayflies and butterflies to the substantial lampreys and eels.

GROWTH AND REPRODUCTION.—Growth, as we have seen, is fundamentally a multiplication of the complex molecules that constitute the living cell. In many-celled organisms this also implies the continual multiplication of cells, for apart from occasional giant-cells, growth is always associated with cell-division; so what in one-celled organisms is termed multiplication or reproduction becomes in many-celled organisms their characteristic process of growth. Thus, for organisms that multiply asexually, it is plain that reproduction is discontinuous growth; and one of the reasons why it must occur is discoverable in cases where a "limit of growth" is reached, that is to say, a definite size, which is physiologically the optimum for the organism concerned. Beyond this limit of growth there is a setting in of some degree of instability; and this is the prelude to reproduction. The detailed physiology is not yet elaborated, but the fact is clear that reproduction tends to occur at the limit of growth, either for the organism as a whole, or for certain parts. In numerous cases, however, the limit of body growth remains indefinite, as in many fishes, reptiles, animal colonies, and plants; and this makes the analysis of reproduction more difficult in the more highly differentiated organisms. Moreover, the periodic occurrence of reproduction cannot be too simply interpreted as the direct result of an instability consequent on reaching a limit of growth; for the regulation of the balance of the body becomes very subtle and imperative, involving, for instance, a periodic activation of hormone-producing tissue in the reproductive organs or gonads. Thus while Haeckel's and Herbert Spencer's dictum that "repro-

duction is discontinuous growth" remains profoundly true, it needs further elaboration, at least in the higher organisms, if not perhaps in all.

The importance of the relation between reproduction and the limit of growth may be illustrated in reference to the cell, or to any compact one-celled organism, such as a spherical Sporozoon or an ovoid yeast-plant. When a growing cell (or unicellular organism) of regular shape, spherical let us say, increases its volume several times, its surface does not increase at the same rate; volume increases as the cube of the radius, and surface only as the square. This disproportion is very important, for it is by the surface that the living matter of the cell is fed, aërated, and purified, in short, kept alive. If the cell goes on growing beyond the limit at which the surface can meet the requirements of the volume of living matter, then instability is inevitable. The regulated way of dealing with this is for the cell to divide into two, thus increasing surfaces in ratio of volumes, and towards growth anew. Thus it is that the reproduction of the cell occurs at the limit of growth. No doubt other factors have to be considered besides the ratio of surface and volume; thus there is the relation between the nucleus of the cell and the general cell-substance—the ratio of nucleoplasm to cytoplasm—so much emphasised by R. Hertwig. There is as yet too little understanding of the precise nature of the instability that directly induces the cell-division; hence the hypotheses implied in terms like "auto-toxic", "enzymatic", cytolytic—each expressing an aspect of the process. There is also difficulty in passing from the consequences of the limit of growth in a single cell to those that apply in the physiological economy of a large animal. Enough here that study of the limit of growth in cells and cell-aggregates throws some light on the physiological necessity for reproduction. As we have noticed in another section, one of the great trends of evolution is towards increase of *internal surface*, and cell-division is one of the deepest expressions of this.

Nutrition and Reproduction.—Another general idea to be kept in mind is the physiological antithesis between nutrition and reproduction. In conditions of abundant food the common Hydra produces many adherent buds, literal reproductions of itself. A bud, while still attached to the parent, may bear buds of its own. Eventually, a check to nutrition occurs; conditions set in which are not favourable to continued assimilation; the buds separate off, and this may be followed by a phase of sexual reproduction.

Similarly a Planarian worm in good nutritive conditions may form asexually a chain of four daughter-worms; a check to nutrition may occur; the links separate; and after a varying period of free life sexual reproduction may set in. There are many illustrations of this organic see-saw between nutrition and reproduction. Vigor-

ously growing fruit-trees have often to be root-pruned, because the check to nutrition favours the reproductive activity which we desire, as flowering and fruiting. But if foliage and vegetative activity is desired, then the flower-buds have to be nipped off to prevent "running to seed". Similarly it is well known that castrated domesticated animals tend to put on flesh and fat—whence ox, capon, and the like. Nutrition and reproduction are thus substantially antithetic. It is not accidental, but fundamental, that the flower oftenest occurs towards the apex or at least well up the vegetative axis, where food-supplies are at a minimum, though this con-

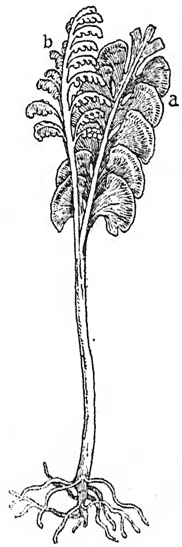


FIG. 59.

The Moonwort Fern (*Botrychium lunare*), showing the contrast between the vegetative frond (*a*) and the spore-bearing fructification (*b*). After Sachs.

sideration is too simple as we have stated it for the moment; for it requires, for instance, to be also correlated with the occurrence of what are called "metabolic gradients".

METABOLIC GRADIENTS.—In Planaria, a simple Turbellarian worm of ponds and streams, the everyday chemical routine or metabolism, as measured by the CO_2 output, etc., is most intense at the anterior end of the body, and gradually wanes to a point distant from the head by about three-quarters of the total length. There the regulative influence exerted by the head is at a minimum, and it is at this point that preparation begins to be made for asexual reproduction and for the development of a second head, which will

be that of the posterior end when that is liberated as a separate worm. Behind this minimum line, the metabolic gradient rapidly rises again, but soon falls towards the tail. There can be no doubt that the physiology of reproduction must take account of areas where the regulative control of other parts wanes away, and where cells remain more free to assert their own individuality, even to the establishment of a new grouping, if not even a new individual, as often happens in Planarian and other simple worms.

Returning to the growing axis of the flowering plant, the growing point is the region with the highest rate of metabolism; and there is a gradual decrease down the stem—a metabolic gradient. Within a variable distance from the growing point a controlling sway is exerted over the incipient buds; they cannot develop until the tip of the stem has grown to some distance away from them. If the growing point is covered with a small cap of plaster of Paris, it loses its physiological dominance, and the buds which were inhibited will begin to develop. If the plaster cap be removed, the development of the buds will stop and the young shoots will die. But if the lateral shoots developing from the buds had been able to outstrip the apex of the stem before the cap was removed, then the inhibition power of their growing points will predominate over that of the apical shoot, which will therefore die. Here then is another set of considerations to be kept in mind in trying to understand reproduction.

Anabolism and Katabolism.—But some attempt must be made to find an intrinsic necessity for the *alternation* of the fundamental processes of anabolic and katabolic preponderance. Multiplication follows growth; reproduction see-saws with nutrition; what is the fundamental reason for this? Can we get below the general proposition that the more a material system accumulates potential energy, the more liable it is to suffer loss—a tendency universal in the physical world, but a tendency which living creatures have been able in large and varying measure to evade.

We have seen how the problem of this alternation, which is of the essence of vital rhythms, has been discussed by Sager, who believes that it is possible "to explain inherent rhythmicity as a physicochemical consequence of the colloidal structure of protoplasm". The protein and other molecules built up in anabolism have an architectural instability proportionate to their complexity. But their breaking down, in which the potential energy of the edifice is changed into the kinetic energy of what may be even a smashing collapse, is happily restrained or resisted by the properties of the viscous, emulsoid, colloidal protoplasm. The nature of this resistance is beyond our scope here, but its effect is to make the discharge of energy intermittent, and in alternation with the anabolic restoration of the molecular architecture. Sager gives a picturesque illustration.

There are, he supposes, two lock-gates in a stream, which are kept in position by powerful springs. The water accumulates above the gates, until there is so great a pressure that the resistance of the springs is overcome and the gates are driven open. After the rush of water has gone through, the springs will come into effective action, and close the gates, until the same sequence has to be repeated. Anabolism corresponds to the accumulation of the head of water; katabolism is the bursting open of the gates and the down-rush; the springs of the gates have their analogues in the colloidal properties of protoplasm. We do not suppose that Sager has *solved* the problem of the alternating preponderances of anabolism and katabolism, but his thoughtful contribution is very welcome. It is something to have seen that there is a problem at all.

In any case, all agree that the chemical routine of living creatures often shows a rhythmic periodicity of winding-up and running-down; that is to say, these alternative processes often show a regular, methodical repetition of varying and even contrasted intensities. Such autonomic rhythms are characteristic of living creatures, and are fundamental to the further and secondary rhythms, which are associated with periodic environmental changes—e.g. diurnal, tidal, or seasonal.

ADAPTATIONS IN REPRODUCTION.—In typical Vertebrate animals, and in many Invertebrates, a rhythm has been established in the body such that reproductive activity sets in at the time of year favourable to the starting of a new generation or a new family. This is, of course, a very complex adjustment; for while it is of great importance that the young should be born at a favourable time of year, this may be secured not only by a change in the pairing time, but also by a change in the duration of antenatal life. Similarly among seed-plants there may be a long or a short interval between the time of pollination and the time of seed-scattering. A seed, too, may remain for a long time quiescent, before it becomes a seedling. The life-histories that are most readily interpreted are those of annual animals and annual plants in countries with well-defined seasons, for summer is then the time of pairing and pollinating, autumn the time of early development and separation from the moribund parent, winter the time of lying latent and well-protected, whether as seed or cocoon, and spring the time of resumed development and youth. But the variations on this theme are wellnigh bewildering. Rats, mice, rabbits, etc., have three or four litters in the year, but this is very different from the state of affairs in not a few short-lived insects which have several generations in a summer. There are slowly developing types, like elephants, "century plants", etc., that are not mature till many years have passed; there are some midges and worms and two or three amphibians that are repro-

ductive even in larval life. Another set of contrasts is disclosed when we compare (*a*) egg-laying animals, whose eggs are fertilised quite outside the body, as in salmon, to take one example out of myriads; (*b*) egg-laying animals, whose eggs are fertilised at the moment of liberation, as in frogs; (*c*) other egg-laying animals, whose eggs are fertilised inside the body, as in birds. Similarly, as to hatching, that occurs outside the mother's body in the oviparous types, e.g. birds and most fishes. In other types the eggs are already hatching as they are being laid, as in some lizards and snakes; and to this the awkward term "ovo-viviparous" is applied. In yet other types the young are liberated from the egg-envelope while they are still within the body of the mother, as in the primitive Peripatus or in the common

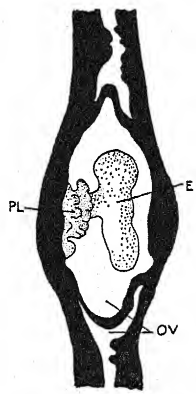


FIG. 60.

Embryo of Peripatus in the Oviduct of the Mother. After Kennel. The embryo (E) is bound to the wall of the oviduct (OV) by a linkage (PL) which is distantly analogous to a mammalian placenta. The young may remain for a year developing within the mother.

Brown Lizard, two widely separated viviparous forms. Taking mammals by themselves, we find that the Monotremes are actually oviparous; the Marsupials are prematurely-bearing, with no true placenta (save a beginning in Perameles). All the other mammals (Placentals) have a more or less prolonged ante-natal partnership between the mother and the unborn young. This is anticipated in the ante-natal placenta-like connections in the oviducts of two dogfishes and in several reptiles; but its perfected development as a complex organ, effecting symbiosis between the mother and the unborn offspring, is restricted to the Placental Mammals; and in various orders of the placental mammals, this important organ has been shown by anatomists to present various phases of evolution.

Thus, broadly speaking, not only has the general development of the mammals been in terms of mothering, but *their* main lines

of development also: the long obsessive insistence on lion or tiger in terms of teeth and claws, and the corresponding low estimate of the apes and monkeys, notwithstanding.

REPRODUCTION AND DEATH.—While reproduction is concerned with the beginning of new lives, it not infrequently involves the ending of the life of the parent. In many organisms, reproduction is the beginning of death. The survival of annual plants to become biennials and perennials is thus one of the most notable advances of plant life. In some relatively simple animals, such as certain Annelid worms, the parent, especially the mother, may rupture and die in liberating the reproductive elements. The case of the Palolo-worms, *Eunice viridis* and others, is of special interest, since the great part of the body, laden with eggs or sperms, is set adrift and liberates these by breaking up in the waves; while the head-end, remaining in the crevice of the coral-reef, regrows its body for the next year's sacrifice. In this case death is evaded. While it is one of the trends of evolution to lessen the physiological strain of reproduction, some insects, such as Mayflies and many butterflies, die a few hours after reproduction; and the same is even true of some comparatively large and strong animals, as lampreys and eels. The exhaustion is fatal and the males are often victims as well as their mates. But among higher animals there is a strong tendency to reduce the sacrifice, not to speak of the fatality, of reproduction. The familiar tragedy of the human mother's death in child-birth must be regarded as altogether abnormal and unnatural.

THE RATE OF REPRODUCTION AND OF INCREASE.—The rate of reproduction depends upon the constitution of the individual organism and on its immediate environment and nutrition. The rate of reproduction in greenflies and rabbits is high; in elephants and golden eagles it is very low. The rate of increase, which is much more difficult to estimate, when a periodic census is not readily practicable, depends upon the wide and complex conditions of life which are often included in the phrase "the struggle for existence". Organisms sometimes exhibit an extraordinary increase in numbers in favourable areas and seasons, witness plagues of voles or locusts; but man's usual experience is that these sudden floods of life are soon arrested. The increase meets checks of famine and weather, and a balance is automatically restored. Even where species are becoming rare and seem dwindling away, the reduction in numbers is usually very gradual and slow, except when man ruthlessly interferes, as in the case of the Great Auk and the Passenger Pigeon, the Quagga and the American Bison. In natural conditions the decrease of the population is occasionally sudden, as in the disappearance of the

Tile-fish (Lopholatilus) for a long stretch of years after 1882, probably as the result of some oceanic cataclysm; but slight fluctuations are the rule. And even the Tile-fish has been reinstated. A sudden increase may bring its own check in the growing scarcity of food; a sudden decrease may relieve the intra-specific competition, so that the mortality of young stages is reduced, and the number of the population is re-established.

In his famous *Essay on Population* (1798) Malthus showed that the increase of human population tends to outrun the means of subsistence, but is met by various "positive" checks (disease, starvation, war, infanticide) and by various "prudential" checks (ethical and economic restraint, which may imply some artificial method of preventing conception). The teaching of Malthus was:

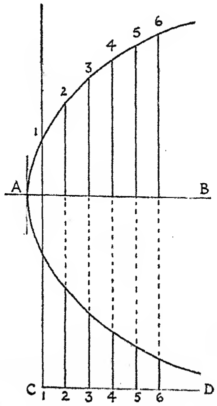


FIG. 61.

Diagram indicating in six different types the inverse ratio of reproduction or genesis (upper perpendiculars, 1–6) to individuation (lower perpendiculars, 1–6).

To avoid the horrors of "positive" checks, put "prudential" checks into operation. This is a large question by itself; we are here most concerned with the fact that the essay of Malthus came as a powerful suggestion to both Darwin and Wallace, who extended the induction to plants and animals, recognising in their increase one of the fundamental conditions of the struggle for existence, and finding the analogues of Malthus's "positive" checks in the various modes of elimination that operate in Natural Selection.

Not less important was Herbert Spencer's analysis of the laws of multiplication. To these we shall return, but the gist of his thesis must be stated here. Including under the term *individuation* all the race-preserving processes by which the individual life is completed and maintained, and under the term *genesis* all the processes that lead to the production of new individuals, Spencer maintained that

individuation and genesis vary inversely. Genesis decreases as individuation increases, but not quite so fast; in other words, progressive evolution in the direction of individuation is correlated with a diminishing rate of reproduction.

Spencer adduced some general physiological reasons why individuation and genesis should vary inversely; he also brought forward inductively a number of instances to show that as a matter of fact poorly individuated types are very prolific, while highly individuated types exhibit economised reproductivity. The tapeworm with its degenerate body and drifting life of ease has its millions of embryos; the Golden Eagle, with its complex body and controlled life, has only two eaglets in a year. There are many facts of this kind showing a coexistence of low individuation and prolific reproduction, of high individuation and small families. The inverse ratio is an observed fact, an outcome of the evolution process. But what Spencer did *not* prove is that high individuation directly lessens fertility. Perhaps it does, but that has not been proved.

REPRODUCTION AND HORMONES.—In a higher animal the reproductive maturity is marked by a multiplication and ripening of the characteristic cells in the ovaries and testes (gonads), which often increase in size at the breeding period, and evoke tumescence in their accessory organs. Especially in the male there is a restless urge to secure the relief that the liberation of the reproductive elements brings. But not less important towards all this is the activation of endocrinal tissue associated with the gonads, the result being the production of sex-hormones, which are distributed through the body by the blood. These gonadial hormones stimulate the development of hitherto latent sex-characters, some of which are ancillary to reproduction. Thus the thumb-like swelling up of the first finger in male frogs is of service in the sexual embrace. Similarly the activation of the milk glands in the female mammal prepares for the future suckling of the young; hormones change the character of the uterus for the fixing of the egg-cell and the establishment of the placenta. So, too, the secondary sexual characters of males, e.g. antlers, manes, beards, etc. There is also in both sexes a marked effect on the nervous system; as at least the liberating stimulus for psychical predispositions previously more or less latent. In highly evolved organisms like birds as well as mammals, it is impossible to ignore the psychological aspect of reproduction, and there are not a few instances of this in many simpler forms as well.

Hormones of the Reproductive Organs.—It was from a study of the stimulating effect of injections of testicular extract that Brown-Sequard was led many years ago to realise the importance of internal secretions in general; and it is fitting therefore that we should give prominence to the inquiry which has developed increas-

ingly during the twentieth century. Moreover, there can now be no sufficiently clear understanding of the phenomena of sex apart from what we may call the "gonadial hormones".

In the first instance the essential reproductive organs should not be called "glands", as has long been the custom, but rather "gonads", for their primary function is the production and liberation of egg-cells or sperm-cells; and cell-multiplication is not a glandular function. Yet the old name "reproductive glands" is more accurate than the critics of the usage knew, for it has been shown that the reproductive organs of Vertebrate animals contain endocrinal tissue which produces "hormones". These pass into the blood-stream and are of profound importance in connection with sex and reproduction.

MALE ORGANS.—In very varied degree in different types there is in the testis a kind of tissue (first noticed by Leydig in 1850) which is usually called "interstitial". From the seasonal variations in the amount of this interstitial tissue, and from other lines of evidence,

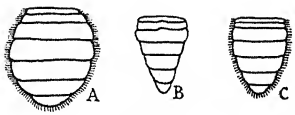


FIG. 62.

Forms of Abdomen in a Crab (Pachygrapsus), castrated by a parasitic Crustacean. After Geoffrey Smith. A, the normal abdomen of the female; B, the normal abdomen of the male; C, the abdomen of the parasitised male, approximating to the female type.

it is highly probable, if not certain, that it produces the specific testicular "autacoid" or hormone.

From ancient times it has been known that removal of the male reproductive organs in early life is followed by the repression of the man's normal masculine characters, such as beard, larger and deeper-toned larynx, and stronger bones. Castration in later life may be followed by retrogression in masculine characters and by the putting on of fat.

Similarly, in other organisms, the removal of the testes prevents or checks the development of the stag's antlers, the cock's spurs, the swollen first finger of the male frog, and so with many other secondary sex-characters. Moreover, the implantation of testes or pieces of testes from another animal, even when inserted in quite irrelevant regions of the body, may have the result of counteracting the check that had set in. Thus Nussbaum found that a castrated frog, which in ordinary circumstances would not develop any swelling on the first finger, did grow the normal pad, used in the sex-embrace, when pieces of testes from another frog were grafted into the dorsal lymph-sac.

Female Organs.—There is not yet any unanimity on the part of investigators as to the presence of "interstitial tissue" in the ovary, but it is generally agreed that an endocrinal function is discharged by what are called the *corpora lutea* in mammals.

An ovarian ovum or egg-cell in a mammal lies within a nest of cells—the Graafian follicle, which de Graaf himself mistook for the ovum itself. When the egg is mature the follicle bursts, and the empty nest is invaded by follicle-cells, which form the *corpus luteum*. If the liberated ovum is not fertilised or is not fixed after fertilisation to the wall of the uterus, the *corpus luteum*, after developing a little, undergoes retrogression and disappears. But if pregnancy occurs, the cells of the *corpus luteum* develop rapidly (filling with lipoid granules of a yellow colour, to which the word "luteum" refers), and a further ingrowth from the wall of the burst follicle establishes connective tissue and blood-vessels. The endocrinal function of the *corpus luteum* then sets in. Its internal secretions evoke changes in the wall of the uterus, which aid in the fixation of the ovum and in the development of the placenta. In some cases it seems to have been proved that the influence of the *corpus luteum* is a *sine qua non* of the ovum's fixation and development. Another function of the *corpus luteum* in the pregnant mammal is the stimulation of the development, and even activity, of the mammary glands.

Many facts point to the conclusion that the ovary of Vertebrates in general produces an internal secretion, analogous to that of the testes, and determining the secondary sex-characters of the female; but the effects of spaying the female are not so marked as those which follow the castration of the male; nor, as we have mentioned, is the seat of the formation of the ovarian autacoid so clear as in the case of the testes. It is probably included as a differentiated part of the connective tissue framework or stroma of the ovary.

Removal of the ovaries tends to inhibit the development of such female organs as the uterus and the mammary glands, and also to induce stoutness.

In some types, such as birds, it seems certain that the inheritance of the female organism includes the potentiality of various masculine characters, whose expression or development is believed to be kept in check by an inhibiting hormone (chalone) from the ovary. This is borne out by the repeatedly verified experiment of removing the ovary from a duck, the result being the assumption of the complete drake plumage at the next moult. Steinach has shown that the implantation of testes in spayed female mammals may bring about the development of secondary male characters, and, conversely, that the implantation of ovaries in a young castrated male (rat or guinea-pig) may induce the appearance of certain feminine characters, notably milk-giving mammæ.

Apart from hormones from the essential reproductive organs of the female, there is evidence of others. The wall of the functioning uterus is credited by some with a hormone that influences the mammary glands and the production of milk. It is also affirmed that the lactating milk gland produces a hormone that stimulates its own activity! Very important, if confirmed, is the theory that the placenta and the fœtus produce moderative hormones that inhibit milk secretion, which begins actively after birth, when the placental and fœtal inhibition has ceased.

Very interesting also, but requiring confirmation, is the probability that just as hormones from the mammalian mother pass through the placenta into the developing young, so from unborn young to mother there may be a passage of hormones which enable her to make the most of her food. Thus the close ante-natal relation of mother and offspring would be a symbiosis indeed.

ILLUSTRATIONS OF THE PROBLEMS OF REPRODUCTION

TELEGONY.—Telegony is a term coined by Weismann to describe the influence of a previous sire on offspring (subsequently borne) by the same mother to a different sire. Thus many dog-breeders are convinced that if a pure-bred bitch has had pups to a mongrel, her value is thereby greatly depreciated; the belief being that she will not afterwards breed true when paired with dogs of good breed. In other words, the influence of the mongrel (the previous sire) is supposed to last, so that subsequent offspring by a pure-bred sire are specifically affected.

To cite a case, we read that "if a pointer bitch gets accidentally served by a collie dog and produces a litter, the pups will be of various types, some like the pointer, some like the collie, and some a blend. And let that pointer bitch be afterwards served by a pure pointer dog, the result will be a litter among which the collie type can be unmistakably observed".

It may seem strange that we should write as if there were any doubt as to the occurrence of telegony, especially since a belief in its reality is translated into £ s. d. among breeders. It is said to occur in horses, dogs, cats, sheep, cattle, pigs, rabbits, rats, mice, and pigeons. There is no doubt as to the occasional occurrence of peculiar phenomena; the question is whether they can be interpreted as evidence of telegony. Thus there is an occasional occurrence of hark-backs or reversions, and there is often a rehabilitation of Mendelian recessives which have remained latent for generations.

But when such things happen and are not understood it is natural that the breeder should lay the blame on some chance crossing. Especially natural will this be when the chance crossing was fol-

lowed by a family. But this is very apt to involve the *post hoc, non propter hoc* fallacy. The breeder makes a scapegoat of the chance sire, whose influence is supposed to "infect the germ" fertilised by a subsequent and reputable father. The only way to certainty is by experiment.

The famous case of Lord Morton's mare (1821), which Darwin discussed, concerned a nearly pure-bred Arabian chestnut mare which bore a hybrid to a quagga, and afterwards produced two colts by a black Arabian horse. These colts were partially dun-coloured, and showed stripes on legs and some other parts. The mane was like a quagga's, being short, stiff, and upright. This seems at first sight very satisfactory, but the drawing of the most quagga-like of the two colts is said to show only indistinct stripes, such as sometimes occur as reversions on pure-bred foals. A stiff mane may also occur as a variation among horses. It is possible that the quagga crossing had nothing to do with the peculiarities of the subsequent pure-bred foals. Prof. Cossar Ewart, with patient and careful experiments, crossing pony and zebra, gave every opportunity, so to speak, for telegony to assert itself, yet with no clear evidence of its reality.

So it has been with other experiments; the evidence has never been quite conclusive. Negative cases do not, of course, prove that telegony never occurs; hundreds of experiments might be necessary before clear-cut positive evidence was forthcoming.

Does telegony occur in man? There are plenty of surmises, but there is no certainty. We hear of a white woman who lived for a while with a negro and afterwards with a white man. The children by the second father had some negroid peculiarities! But man's standard of accuracy—not to speak of veracity—is not high in regard to these matters.

Prof. Karl Pearson has approached the problem from the statistical side. If a female can be influenced in a telegonic way by a previous mate, should there not be in permanent unions of a pair an increasing influence from the father's side? But there seems to be, as regards stature, no such evidence of any increase in the influence of the father on a series of children.

It is much to be desired that those who live near the overlapping of distinct races should look out for suggestions of telegony in cases where the same mother has offspring first to a husband of one race, and afterwards to a husband of another race. Faithfulness to the second husband would obviously have to be presupposed if the case was to have any scientific value. An easier set of observations might be made at home by comparing the families of the same mother by two successive husbands. Does the first husband continue to count?

Although we are not sure that telegony is a fact, various theories

have been suggested to account for it! The best of these theories, applicable to mammals only, is very interesting. Suppose a mammalian mother begins, as the result of insemination, to develop an offspring, there is an ante-natal period, eleven months in a mare, during which the developing embryo lives in very intimate partnership with its mother. By means of the placenta, binding the unborn offspring to its mother's womb, there is exchange of dissolved substances between the two. Food, oxygen, and hormones pass from the mother into the embryo; nitrogenous waste-products, carbon dioxide, and hormones pass from the embryo into the mother. But the inheritance of the developing embryo is paternal as well as maternal, and therefore the influence of some striking paternal characteristics may pass back from the embryo (e.g. as hormones in the blood) and influence in some specific way the constitution of the pregnant mother. In a subsequent pregnancy due to another father, the specifically altered constitution of the mother may exert a definite influence on the new offspring; and this would be telegony. This seems to be a physiological possibility, though it is more roundabout than used to be supposed.

GRAFTS AND CHIMÆRAS.—From ancient times fruit-growers have practised grafting with great success. A common form of the device (for it is effected in several distinct ways) is to insert a young shoot of some desirable fruit-tree into the stem—often lopped—of a sturdy one, taking care that the embryonic tissue (cambium) and the young sap-wood of the two plants are brought firmly together so that genuine physiological fusion results. The engrafted bud or shoot is called the "scion", and it is made to combine with a "stock". In this way a variety of fruit-tree that is marked by great excellence can be quickly and surely multiplied, for the essential fruiting virtues of the scion are not affected by the vigour of the sturdy stock, though its vegetative growth may be checked. But even this checking is an advantage when the object in view is to get much fruit. Thus we see fine orchards with the high-class engrafted young trees bearing very abundant and conveniently reachable fruit on the shoulders of the inconspicuous old-fashioned stocks. Scion and stock must be near relatives; thus the peach may be grafted on a plum stock, the apricot on an almond, the apple on a pear, the pear on a quince, the medlar on a hawthorn, and so on. In modern times grafting of succulent plants has been successfully effected, but most grafts are between trees. It is possible that the idea of grafting was suggested to the early fruit-growers by noticing that two branches of the same tree, or even of adjacent trees, sometimes fuse when they are so much rubbed together by the wind that two abraded surfaces are formed, and a mending of the mutual wounds results in a thoroughgoing fusion.

For some grafts it must be admitted that the scion is affected in a general way by the stock, e.g. as regards the time of flowering; and the stock may be in some measure reinvigorated by the growth of its nobler scion; but the notable point is that each retains its characteristic features. There are, however, some puzzling cases of a different type, which suggest that there may be a mingling of the characters of scion and stock. In other words, there are alleged cases of "graft-hybrids"; and the most famous of these concerns the Common or Yellow Laburnum (*Cytisus Laburnum*) and the allied Purple Laburnum (*C. purpureus*). When a scion of the purple species is engrafted on the yellow, the resulting growth or a cutting therefrom usually bears purple flowers, as an ordinary graft would do, but along with these there are others that are yellow. In some other ways the plant, which was called Adam's Laburnum (*C. adami*) resembles *both* the yellow and the purple species; and Darwin called it a "graft-hybrid". It interested him greatly, and he speaks of "the extraordinary fact that two distinct species can unite by their cellular tissue, and subsequently produce a plant bearing leaves and sterile flowers intermediate in character between the scion and stock". But, as will be explained later, it seems likely that Adam's Laburnum is even stranger than Darwin supposed.

A clue has been found by studying some other grafts, such as that effected between the tomato (*Solanum lycopersicum*) and the Deadly Nightshade (*Solanum nigrum*), the repetition of the technical names being useful to emphasise the fact that the two plants are species of the one genus, Solanum, to which the potato also belongs. Now the shoot that grew from the artificially effected graft combined the characters of both stock and scion. Sometimes the result was more like a tomato, sometimes more like a nightshade, sometimes nearly intermediate between the two. So it looked like a graft-hybrid, and it received the name *Solanum tubingense*. It is not sterile, as Adam's Laburnum is, and its seedlings revert to one or other of the "parent" forms.

But some of the results of the grafting of tomato and nightshade look rather different from those to which we have just referred, for one part of the shoot is like the scion and another part is like the stock. This is what is meant by a "chimæra", two living creatures intimately combined, yet each retaining its intrinsic peculiarities. Even when the result of the graft looks very like a blend, a minute analysis may show that here is a sort of patchwork combination of the two components. And if so, it is rather a chimæra than a graft-hybrid. In fact, it is beginning to be doubtful whether there are any graft-hybrids at all.

Familiar in gardens and greenhouses are Pelargoniums with white-margined leaves, and some of these are due to grafting and to vegetative propagation from the results of the graft. In this strange

case, one partner forms the main body of the plant, while the other partner forms the skin only, or the epidermis plus the hypodermis. This strange mosaic is a type of chimæra, and recent investigation has shown that Adam's Laburnum, whose secret we have been deferring, is another dual plant or chimæra, the main body being that of a Yellow Laburnum, while the skin is that of the purple species.

Homer's chimæra had the head of a lion, the body of a goat, and the tail of a dragon; and others depicted in ancient literature and heraldry were similarly impossible combinations. The zoologist's Chimæra (e.g. *C. monstrosa*), is a remarkable fish, sometimes caught off British coasts, which the fishermen curiously call the "shimmer"; and it probably owes its technical name to the impression that it is a sort of impossible combination of characters.

But there are in the Animal Kingdom a few genuine chimæras in the technical sense—mosaics that man has made. Unfortunately, as regards impressiveness, they are mostly confined to early youth, and they are all very small when compared with Adam's Laburnum.

It is not very difficult to graft a piece of one animal on to another of a related species. Serious wounds have sometimes been mended in this way, and everyone knows of the transfusion of blood. There is nothing chimerical about this.

On the other hand, it is possible to graft together the very early stages of two different species of newt (e.g. *Triton cristatus* and *T. tæniatus*), with the result that they combine harmoniously and go on developing, each keeping to its own species! And just as in the plant world, so among these amphibians, the chimæras are of two kinds. A region of the young animal, perhaps a whole side, may be of the one species; while another region, or, it may be, side, is just as clearly of the other species. This is called a "sectorial" chimæra. In other cases, reminding one of the Pelargoniums, the skin belongs to the scion and the rest of the body to the stock. This is called a "periclinal" chimæra. In both types of amphibian chimæra there is a combination, but not a mingling, of the two components. Another chimæra has been made by artificially combining the stalked freshwater polyp, Pelmatohydra, and the ordinary unstalked Hydra. They combine intimately and get on well together, but they do not in any sense mix. It sounds rather chimerical, but there it is.

CONSANGUINITY.—When we speak of a consanguineous union, we mean that the two organisms are near relatives; when we speak of a high degree of consanguinity in a herd or in a community, we mean that there has been much in-breeding or endogamy. In regard to the results of this sex-union of closely consanguineous organisms, it must be admitted that clear-cut facts are few. It should also be noted that, as the range of living creatures expresses a very long

gamut, we must be very careful in arguing from one level to another. What is normal and apparently wholesome at one grade may be very undesirable at another.

It has been securely established that some hermaphrodite animals habitually fertilise their own eggs. This "autogamy" has been proved in some tapeworms and flukes—not auspicious illustrations; it seems sometimes to occur in the freshwater Hydra and a few other free-living animals. There are numerous self-fertilising flowers, though there is no case known where cross-fertilisation is impossible. It may also be that one hermaphrodite liver-fluke sometimes inseminates another, so that the habitual autogamy may be interrupted. In the great majority of hermaphrodite animals, such as earthworms

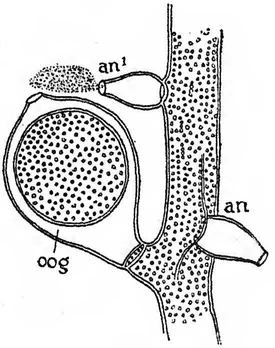


FIG. 63.

Male and Female Organs of a Simple Alga (Œdogonium). *an'*, antheridium liberating spermatozoa; *oog*, female organ or oogonium containing an ovum; *an*, an antheridium empty.

and snails, cross-fertilisation is the invariable rule. It is also relevant to recall the fact that in many of the small Crustaceans, in many Rotifers, and in some insects, such as Aphides, there may be long-continued parthenogenesis—generation succeeding generation without loss of vitality, although the eggs develop without any fertilisation. In some of the Rotifers the males are still undiscovered; Réaumur kept Aphides breeding parthenogetically for over three years (50 consecutive generations), and Weismann kept females of a common water-flea (*Cypris reptans*) breeding in the same way for eight years. This shows that at certain levels of organisation a vigorous life may be kept up for many generations, not only without any introduction of "fresh blood", but without the presence of any males.

A number of careful experiments have been made on inbreeding, but there is imperative need for more. Weismann in-bred mice for twenty-nine generations, and his assistant, Von Guaita, continued

the experiment for seven more generations, but the only notable general result was a reduction of the fertility by about thirty per cent. Some experimenters, such as Crampe, have found that the inbreeding of rats resulted in disease and abnormality, but this was not observable in equally careful experiments made by Ritzema-Bos. He in-bred rats for thirty generations; for the first four years (twenty generations) there was almost no reduction in fertility; after that there was a very marked decrease of fertility, an increase in the rate of mortality, and a diminution of size. These and other experiments on mammals suggest that very close in-breeding may be continued for many generations without any observable evil effects and, on the other hand, that there are limits beyond which inbreeding becomes disadvantageous. It is certain that, if there be well-defined hereditary predisposition to disease in the stock, then in-breeding soon spells ruin.

Extensive experiments by Castle and others (see *Proc. Amer. Acad.*, xli. 731–786) on the inbreeding of the pomace-fly (*Drosophila ampelophila*) led to the general result that "inbreeding probably reduces very slightly the productiveness of Drosophila, but the productiveness may be fully maintained under constant inbreeding (brother and sister) if selection be made from the more productive families".

Some of the histories of domesticated breeds are so well recorded that they may be ranked as carefully conducted experiments, and it seems that some very successful breeds of cattle—such as Polled Angus—have in their early stages of establishment involved extremely close inbreeding. When we examine the pedigrees of famous bulls and stallions, we find in some cases an extraordinarily close consanguinity. Valuable results have often been attained by using the same stallion repeatedly on successive generations.

From breeding experiments four general results seem to be clear: (1) that progressive results have usually followed mating within a narrow range of relationship; (2) that close inbreeding tends to fix characters, developing "prepotency"; (3) that close inbreeding may go far without any injurious effect on physique; but (4) that, if there be any morbid idiosyncrasy, close in-breeding tends to perpetuate and augment it.

Darwin paid much attention to the question of inbreeding (see his *Variation of Animals and Plants under Domestication*), and his general conclusions were:

"(1) The consequences of close interbreeding carried on for too long a time are, as is generally believed, loss of size, constitutional vigour, and fertility, sometimes accompanied by a tendency to malformation. (2) The evil effects from close interbreeding are difficult to detect, for they accumulate slowly and differ much in degree in different species, whilst the good effects which almost

invariably follow a cross are from the first manifest. (3) It should, however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour."

From his researches on flowering plants, Darwin concluded that there was "something injurious" connected with self-fertilisation; and although he came to recognise that self-fertilisation was more frequent and more successful than he had at first believed, he adhered on the whole to the aphorism, "Nature abhors perpetual self-fertilisation". In his book on *Cross and Self-Fertilisation* (1876), however, he says: "If the word 'perpetual' had been omitted, the aphorism would have been false. As it stands, I believe that it is true, though perhaps rather too strongly expressed." His general conclusion was that self-fertilisation in flowers is for the most part relatively, but not absolutely, injurious.

There is little biological evidence to show that there is anything necessarily disadvantageous or dangerous in close consanguineous unions. These seem often to occur in nature in isolated and restricted areas, and they are frequent in successful breeding. It must be admitted that evil effects *sometimes* follow prolonged consanguineous pairing in the artificial conditions of stockbreeding, but it must not be hastily inferred that these evil effects are necessarily due to the consanguinity. There may be persistence of unwholesome conditions of life which have a cumulative evil effect as generation succeeds generation, or there may be some organic taint in the early members of the stock which becomes aggravated, just as a desirable organic peculiarity may be enhanced.

Bateson expressed the view of most biologists when he said:

"It should perhaps be pointed out categorically that nothing in our present knowledge can be taken with any confidence as a reason for regarding consanguineous marriage as improper or specially dangerous. All that can be said is that such marriages give extra chances of the appearance of recessive characteristics among the offspring. Some of these are doubtless bad qualities, but we do not yet know that among the recessives there may not be valuable qualities also" (*Mendel's Principles of Heredity*, new edition, London, 1909, p. 226).

The whole subject has been illumined by East and Jones in their fine work, *Inbreeding and Outbreeding* (1919). It is convincingly shown that inbreeding of good stock, accompanied by judicious elimination of "wasters", *fixes* desirable characters, and tends to a stable and uniform herd. That it is sometimes associated with reduction of vigour, resisting power, fecundity, and even size, cannot be denied. But this is not because of the consanguinity as such, but because the inbreeding automatically brings into expres-

sion a number of undesirable "recessive" characters, hidden in conditions of exogamy by their "dominant" counterparts.

Yet this exposure of undesirable features may be utilised by the breeder for the useful purgation of the herd.

On the other hand, there is no doubt that when the same undesirable feature occurs on both sides of the house, inbreeding tends to diffuse and exaggerate it.

The value of exogamy or outbreeding is twofold. It provokes variations and thus increases the range of raw material on which selective agencies can work. It also promotes "hybrid vigour" by the pooling of diverse hereditary resources of good quality. The crossing also makes it more likely that a minus on one side will be made good by a plus on the other, or that desirable dominants will strengthen one another's hands.

When we take into account such evidence as there is from animals and from plants, and such studies as those of Huth (*Marriage of Near Kin*, 1887), and the instances and counter-instances of communities with a high degree of consanguinity, we are led to the conclusion that the prejudices and laws of many peoples against the marriage of near kin rest on a basis not so much biological as social.

In regard to the marriage of full cousins, the likelihood of unhealthy offspring will be very great if there are the same hereditary taints in the lineage of both parents. If there is a well-defined family predisposition to certain diseases, the fact that the marrying cousins are themselves somatically healthy does not justify them in becoming parents. If two somatically healthy cousins belonging to a tainted lineage have what the Mendelians call a single or simplex dose of the taint, the probability is that on the average one-quarter of their children will be similarly tainted. On the other hand, if the family history is good on both sides, there is no biological reason why two healthy cousins, who fall in love with one another, should not marry joyously, or why they should not have wholesome children.

Lunar Periodicity in Spawning.—In ancient Greece and Rome there was a general belief, still lingering locally among Mediterranean fishermen, that various marine animals, such as crabs and sea-urchins, are "full" at full moon and "empty" at new moon. This interesting belief has been recently tested by Mr. H. Munro Fox. He finds that the belief is based on fact so far as the sea-urchins of the Red Sea are concerned, but that it does not hold at all for those in the Mediterranean. In neither sea does it hold for crabs or for mussels.

The reproductive cycle of a Suez sea-urchin (*Centrechinus setosus*) shows marked lunar periodicity. At each full moon during the

breeding season there is spawning. Thereafter a fresh crop of genital products is developed, to be spawned at the ensuing full moon. One and the same individual may become sexually mature at consecutive lunar periods. Another sea-urchin (*Strongylocentrotus lividus*) was observed at Alexandria, Naples, Marseilles, and Roscoff, but it showed no lunar periodicity.

It is difficult to suggest how the lunar changes can affect the sea-urchin Centrechinus in times of spawning at Suez. Mr. Fox has found that the oxygen-consumption of pigmented animal tissues is greater in light than in darkness, and he suggests that if moonlight has sufficient intensity to cause this effect, this may be the reason for the lunar periodicity in the spawning of the Suez sea-urchin. This clue is being followed.

Endomixis.—For eight years or more Prof. L. L. Woodruff, of Yale, has been able to keep agoing a "pure line" of Paramœcium, all descended from one by asexual fission, continued for hundreds of generations. In such a "pure line" there is no conjugation such as has been already described. But, while conjugation does not occur, Prof. Woodruff and Miss Erdmann discovered that there is a monthly occurrence of a remarkable process which they have called "endomixis". In this process, which is like the prelude to conjugation, the nuclear apparatus is scrapped and then reorganised. It seems to have a rejuvenating effect.

It seems that both conjugation and endomixis are able to meet the emergency of physiological degeneration, which may be induced, for instance, by deteriorative environmental conditions. The process of endomixis was discovered in an artificially isolated "pure line", but Woodruff has found that it also occurs in free natural conditions in the species *Paramœcium aurelia* and *P. caudatum*, and it is surely not without significance that these two species are very widespread and are able to exist under very diverse environmental conditions. They have got possession of a secret of rejuvenation—which seems to be in its external aspects like scrapping the organisation and reconstructing it afresh.

How Spermatozoa Reach the Ova.—Here is one of the simplest of questions: how it is that spermatozoa, introduced by the male into the lower part of the female genital tract, manage to make their way to the upper part of the oviduct, such as the Fallopian tube. It was in 1843 that Martin Barry, a medical student in Edinburgh, was first able to demonstrate for a mammal (the rabbit) the fertilisation of the ovum by a spermatozoon within the oviduct, but how the spermatozoa reach the ova is still obscure. The interior surface of the female duct is lined with cilia, which beat vigorously towards the distal end, and are reasonably believed to assist in the downward passage of the egg-cell, in a bird, for instance. But if

the cilia beat strongly towards the lower end of the duct, how do the microscopically minute spermatozoa make their way against the stream?

Various suggestions have been made. Thus it is said that the constitution of the sperms is such that they go against a current, just like elvers going up the river. In other words, their tropism is to move against a current; and of this there is some experimental evidence in cases where the current is not too strong. But here it is interesting to notice the remark of Prof. G. H. Parker of Harvard,

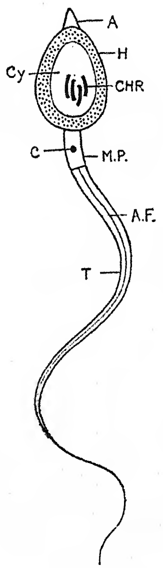


FIG. 64.

Diagram of Typical Spermatozoon. A, peak or acrosome; H, head, containing a minimal amount of cytoplasm (CY) and a number (4) of chromosomes; MP, the middle piece, including the centrosome (C); T, the tail, with axial filament (AF).

whose investigations are always very suggestive: "No one can have examined the ciliary current in a living oviduct without having been impressed by its vigour. In fact, so strong is it that I have never been able to convince myself that spermatozoa could make headway against it, and yet these cells must, by one means or another, reach the proximal end of the oviduct in the neighbourhood of which the egg is fertilised."

It has also been suggested that the seminal fluid may bring about a reversal of the ciliary current, so that it helps the spermatozoa up the oviduct. Such a reversal is known in other cases, but there is no experimental proof that it occurs in the oviduct.

Nor is there any proof that muscular movements of the wall of the oviduct itself are able to force the sperms in the effective direction.

Faced by these difficulties, Prof. G. H. Parker has recently studied the oviduct of the Painted Turtle (*Chrysemys picta*), and has made an interesting discovery. The oviducts of the turtle possess two systems of cilia: a general system covering most of the interior of the duct and beating away from the ovary (abovarian system), and a restricted narrow tract of cilia extending the length of the duct and beating toward the ovary (proövarian system). Thus spermatozoa reach the ovarian end of the oviduct not by their own activity, nor by the muscular movement of the oviduct, nor by the reversal of the ciliary beat in this duct, but by transportation afforded by the proövarian ciliary tract.

Painted Turtles may seem rather remote, but the next step is, of course, to discover whether there is a double ciliary system in the oviduct of birds and mammals. If the down-current is too strong for spermatozoa to make their way against the stream, then we do not know how the intimate fertilisation is effected in sheep and cattle and horses and poultry. But if Parker's discovery of a narrow tract of proövarian cilia in the turtle is corroborated in mammals and birds, then another obscurity disappears.

Fertility of a Female Mule.—One of the miscellaneous items of incorrect information that the man in the street rarely fails to possess is that "mules are always sterile". For ordinary mules (offspring of male ass and mare) sterility is usual in both sexes, and perhaps universal in males, but it is *not invariable* in females. Thus in the third part of Volume V of the *Annals of the Natal Museum* (1926), Dr. Ernest Warren gives details as to the fertility of a female mule. It was the result of a cross between a jack-donkey and a dark chestnut mare, and came in foal to a hackney stallion. The characters of the foal show a remarkable combination of horse and ass characters, varying from nearly complete dominance of either to perfect blending.

Stickleback's Eggs.—In regard to many common animals our knowledge of the reproductive processes is still very incomplete, not to say patchy. Thus we cannot even tell a consecutive story of the breeding habits of the Three-spined Stickleback (*Gasterosteus aculeatus*), which occurs commonly in fresh water, but is able to thrive in the sea as well. As is well known, the male makes a little nest of pieces of freshwater plants, fastened by glutinous threads secreted from the kidneys at the breeding season—a good instance of a more or less pathological process that has become in this case normalised. Several females lay their eggs in one nest, which is valiantly guarded by the one male; and there are eventually 120–150 eggs altogether. This is a very small number for a fish,

but the reproductive economy is obviously correlated with the high development of parental care.

W. Köhler has recently taken the trouble to count the eggs in the ovary of a mature stickleback, and found in March 302 that were ripe, and at least as many that were unripe. Three other females contained 100, 200, and 228 ripe or nearly ripe ova—much larger numbers than were previously reported. Since a well-filled nest contains 120–150 eggs, it seems probable that if the male is polygynous, the female is polyandrous. In other words, it looks as if the female must deposit eggs in several nests. And here it may be

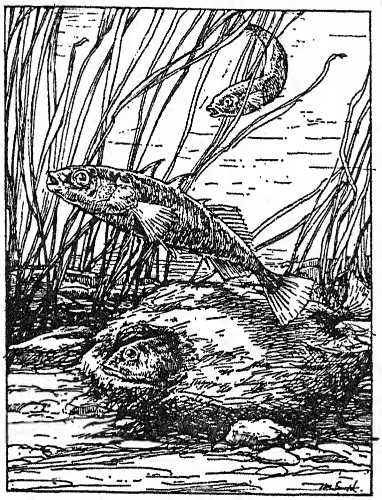


FIG. 65.

The Three-spined Stickleback (*Gasterosteus aculeatus*), and its Water-weed Nest, built by the male on the floor of the pool. The head of the female is seen protruding from the nest, in which she hastily deposits a few eggs.

noted that one would like to know definitely whether the female survives the reproductive strain. Köhler thinks that the unripe eggs observed in March are deposited at a second breeding period in July. He notes that male sticklebacks were seen guarding their nests in July and August, while swimming around them there were half-grown individuals, presumably of the first brood.

FURTHER ILLUSTRATIONS OF PROBLEMS OF REPRODUCTION

PARTHENOGENESIS is the development of an egg-cell that has not been fertilised. A familiar case is that of drone-bees, which

develop from unfertilised eggs; and the prolific summer generations of greenflies or Aphides are parthenogenetic, no males occurring for months. Parthenogenesis is of frequent occurrence (1) in many of the lower crustaceans, such as the brine-shrimp Artemia, the large freshwater Apus, and some small "water-fleas", e.g. Daphnia, Moina, Cypris, and Candona; (2) in some insects, notably among the gall-wasps (Cynipidæ), in certain species of which males have never been found, and among saw-flies (Tenthredinidæ); and (3) in most of the minute Rotifers or "Wheel Animalcules." In most rotifers, parthenogenesis is the rule; in some species males have never been found; in some forms in which they occur they do not fertilise the eggs. In most of the cases of parthenogenesis among crustaceans and insects, males are absent for months or years, but reappear at intervals. Among plants there are few examples of uninterrupted or complete parthenogenesis in the strict sense, for it is necessary to exclude relapses into asexuality, as seen for instance in many of the lower Fungi, where the sexual reproduction has more or less degenerated. The development of an egg-cell without fertilisation is seen in *Chara crinita*, one of the water-stoneworts, which is represented in Northern Europe by female plants only. Parthenogenesis has come to be the rule in the common dandelion, and it also occurs in some hawkweeds and in a few other types, e.g. species of Alchemilla and Antennaria. It may be noted here that there is no reason whatever to associate the dominance of parthenogenesis with any loss of racial vigour. A hundred successive parthenogenetic generations have been carefully observed in the case of Daphnia, and there was no suggestion of any degeneration. In a few cases the occurrence of variation in forms produced parthenogenetically has been demonstrated.

It may be useful to distinguish several different grades of parthenogenesis. (*a*) What may be called *pathological* parthenogenesis is illustrated when the egg-cell, say of a hen, exhibits without fertilisation a number of divisions. In none of these cases has the development been known to go far. (*b*) The term *casual* parthenogenesis may be applied to cases where the occurrence is observed as a rare exception, e.g. in silk-moths. It occasionally happens that worker-ants, not normally reproductive at all, produce ova which develop parthenogenetically. Since the discovery of what is called "artificial parthenogenesis" (see below), these instances of pathological and occasional parthenogenesis have become more intelligible. (*c*) *Partial* parthenogenesis is well illustrated by hive-bees. The queen receives from the drone a store of male-elements or spermatozoa, and it rests with her, in laying the eggs, to fertilise them or not. Those eggs that are fertilised from the store of spermatozoa in her spermothecæ develop into workers or queens (according to the nurture); those that are not fertilised develop into drones. The same is true of some

other Hymenoptera, such as ants. (*d*) The term *seasonal* parthenogenesis may be applied to cases like greenflies or Aphides, where one parthenogenetic generation succeeds another all through the summer, but males reappear in the autumn and fertilisation occurs. This is also illustrated by some of the water-fleas. (*e*) The term *juvenile* parthenogenesis may be applied to some curious cases (e.g. in the midge Miastor) where larval forms exhibit precocious reproductivity without any fertilisation. It becomes difficult, however, to draw a line between such cases and multiplication by means of spores, such as is seen in the larval stages of the liver-fluke and in many plants. Spores are specialised reproductive cells which develop without fertilisation; they are familiar to everyone on the fronds of ferns. The formation of spores is a primitive mode of reproduction, but the parthenogenetic development of ova is probably in all cases secondary and derivative—a relapse from the normal spermic development. None the less it seems to work well in certain kinds of organisms and in certain conditions of life.

It may be asked whether egg-cells which normally develop without being fertilised are in any way different from ordinary ova. But the answer is not at present very clear. In some cases (ants, bees, and wasps) the ova go through the ordinary process of maturation, involving a reduction of the number of nuclear rods or chromosomes to half the normal number. In some other cases (Rotifers, some water-fleas, and greenflies) there is no reduction when the conditions of life are favourable, though there may be when they are unpropitious.

ARTIFICIAL PARTHENOGENESIS.—Of interest is the fact that in a variety of cases the ovum may be artificially induced to develop parthenogenetically. The demonstration of this has been mainly due to Jacques Loeb and Yves Delage. If the unfertilised eggs of a sea-urchin be left for a couple of hours in sea-water, the composition of which has been altered (e.g. by adding magnesium chloride), and be then restored to ordinary sea-water, many of them develop into normal larvæ. A mixture that Delage found to be very effective for sea-urchin ova consisted of 300 c.c. of sea-water, 700 c.c. of an isotonic solution of saccharose, 15 centigrams of tannin dissolved in distilled water, and 3 c.c. of normal ammoniacal solution. It works equally well if the volume of the sea-water or of the saccharose be doubled. The ova were left for an hour in the mixture, then washed several times, and then placed in sea-water, where they soon developed. In a few cases fully-formed sea-urchins have been reared. There are two points of special importance: first, that the artificial parthenogenesis has been induced in a great variety of types, e.g. sea-urchin, starfish, marine worm, mollusc,

fish, and even amphibian; and second, that the artificial stimuli effectively used are very varied—chemical, physical, and mechanical. Artificial parthenogenesis has been induced by altering the chemical composition of the water by adding or removing certain salts, or by altering the concentration by adding salt and sugar, or by subjecting the ova to various influences, such as superabundance of carbon dioxide, vapour of chloroform, ether, benzol, and toluol, the presence of butyric acid, blood, serum, and extracts of foreign cells, or by exposing the ova to electric currents, or to mechanical stimulation. Bataillon has shown that frog's eggs pricked with a needle and washed with blood may proceed to develop rapidly and normally. In a few cases the parthenogenetic development has been successfully carried beyond the completion of the tadpole metamorphosis. The effective stimuli, such as have been enumerated above, differ for different kinds of eggs and even for eggs of the same kind at different stages of ripeness. There is probably some common factor in all the effective stimuli, but what it is remains uncertain.

It is too soon to make more than a tentative statement as to what happens in artificial parthenogenesis. According to some, the artificial changes in the medium do not in themselves directly induce segmentation, but modify the intimate constitution of the egg in such a way that when it is returned to its natural medium, it becomes auto-parthenogenetic. According to Loeb, the physico-chemical agency induces the formation of a "fertilisation-membrane" by a change in the surface of the egg comparable to that which follows the entrance of a spermatozoon. The first step is a cytolysis or partial solution of the cortical layer of the ovum, perhaps a liquefaction of fatty substances in the cellular emulsion. The result is the formation of the "stabilising envelope" or "fertilisation membrane". But the appearance of this membrane seems to lead to an acceleration of the oxidations going on in the egg; the egg is activated and segmentation begins. But this may simply lead to disintegration, if there is not also a corrective factor, and it has been possible to devise experimental conditions that induce activation only and others that induce activation followed by stable development. Thus the presence of a fatty acid, such as butyric, may bring about membrane-formation and the activation of the egg, while the presence of a hypertonic solution (i.e. with increased osmotic pressure) may serve as the essential corrective. The life of the activated egg may also be saved by putting it after the membrane-formation for about three hours into sea-water practically free from oxygen or containing a trace of potassium cyanide. In either way the over-active oxidations in the egg may be suppressed. If the eggs are thereafter transferred into ordinary sea-water containing free oxygen, they often develop normally.

Similarly, pricking the ovum of a frog or toad with a platinum needle and the entrance of several blood corpuscles may serve to activate, while the return to the normal medium may serve as the indispensable corrective to disintegration.

One must not conclude that the rôle of the complex living spermatozoon is exhaustively replaced by the chemico-physical agencies referred to, for normal fertilisation implies more than activation and a regulation of the subsequent cleavage. It implies a mingling of the heritable qualities of the two parents. What the experiments show is that the ovum is quite complete in itself, that certain factors involved in what the spermatozoon effects may be artificially mimicked, and that perfectly normal larvæ may be reared from various unfertilised eggs which are not known ever to develop parthenogenetically in natural conditions. The remarkable facts that have come to light since 1899 show that one cannot set limits to the possibility of the occurrence of parthenogenesis. Some of the experimental conditions which are effective in inducing parthenogenetic development might find a parallel in natural conditions. As yet, no instance of either artificial or natural parthenogenesis has been observed in the animal kingdom above the level of Amphibians.

SEX-DIMORPHISM

Since the beginning of the present century the difficult problem of the origin, evolution and development of sex-characters has been illumined by a series of brilliant experimental researches, which have made reconsideration imperative. This revision has been facilitated by the masterly work of Kammerer (*Ursprung der Geschlechtsunterschiede*, 1912), who gathered together the data and submitted them to an analysis, at once fair-minded and critical. We shall state his conclusions and indicate where we differ from them.

It is usual to classify the differences between the sexes as "primary" and "secondary". The "primary" differences refer to the reproductive organs or gonads, the "secondary" to those that appear in other parts of the body, such as the larynx or the hair. It is clearer to follow Poll, Kammerer, and others in recognising (*a*) essential or gonadial differences which must be present if there are sexes at all—the differences between ovaries and spermaries; and (*b*) accessory differences which may or may not be present, some of them subsidiary to the reproductive organs, either internally or externally, and others affecting extra-genital parts of the body. Our scheme of classification, slightly modified from Poll's and Kammerer's, may be thus expressed:

SEX DIFFERENCES.

I. Essential or Gonadial. . . . In the reproductive organs proper.

II. Accessory or Incidental:

(*a*) subsidiary to the gonads: either internally, as in accessory glands; or externally, as in pairing organs, egg-laying organs;

(*b*) somatic or extra-genital: either internally, as in vocal organs; or externally, as in colour, hair, feathers, etc. Both kinds of accessory sex differences may be controlled in their expression by special hormones liberated from the gonads.

FIG. 66.

Sex Dimorphism in Birds of Paradise. The lower bird is the decorative male and the upper the plain female of *Paradisea minor*.

The sex differences have a structural and a functional side, a morphological and a physiological aspect, but for practical purposes one side may often be disregarded. Thus a chitinous decoration on a male beetle has no vital activity after it is formed; it is the structural side that is important. On the other hand, the differences in the blood of a male and a female, which are of great importance, may not have any detectable structural expression. In a few insects there is actually a difference in the colour of the blood. Similarly, there are many subtle differences in instincts and impulses, in

physiological habit and length of life, which are very real, though we cannot say much about their structural expression!

Another consideration to be kept in mind in the classification of sex differences is the degree of permanence in their expression. An adult peacock can never be confused with a peahen, but there are many birds, e.g. some ducks, which show great dissimilarity between the sexes at the breeding season and great similarity at other times. In many fishes, such as sticklebacks, the males are conspicuously different from the females at the breeding time, but inconspicuously different at other times. In short, there are many nuptial characters which wax and wane according to the sexual state of the organism.

ILLUSTRATIONS OF SEX-CHARACTERS.—Convenient surveys of sex differences are to be found in Darwin's *Descent of Man*

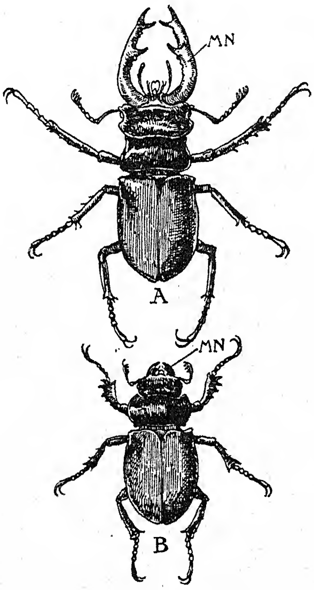


FIG. 67.
Male (A) and Female (B) of the Stag-beetle (*Lucanus cervus*), from specimens. MN, mandibles, which are enormously exaggerated in the male.

and Cunningham's *Sexual Dimorphism* and our *Sex* (Home University Library). Among Mammals one recalls the gorilla's sagittal crest, the mandrill's enormous canines, the elephant-seal's nasal proboscis, the lion's mane, the narwhal's tusk, the stag's antlers, the duckmole's spur. Among Birds one recalls the peacock's tail, the wing-feathers of the Argus Pheasant, the decorations of Birds

of Paradise and humming-birds, the tail of the lyre-bird, the neck-feathers of the ruff, the cock's spur, the great bustard's inflatable throat-pouch. Among reptiles there are a few cases like the erectile dorsal crest of *Anolis cristatus* and the bony horns of some chamæleons. Among amphibians there are the dorsal crests of some newts, the swollen first fingers of frogs and toads, the resonating sacs of some frogs. Among Fishes, we recall the old male salmon's hooked lower jaw, the brilliant colouring of the male dragonet, the "claspers" of Selachians. Among Invertebrates, there are well-known contrasts between the sexes in the Argonaut, in the Giant Japanese crab, in many spiders, in Dynastid and Lucanid beetles, and in many Lepidoptera. Cunningham notices the dimorphism in Nereis, and the case of the female Bonellia with her pigmy mate is famous.

In most cases the positive character is on the male side. He has an

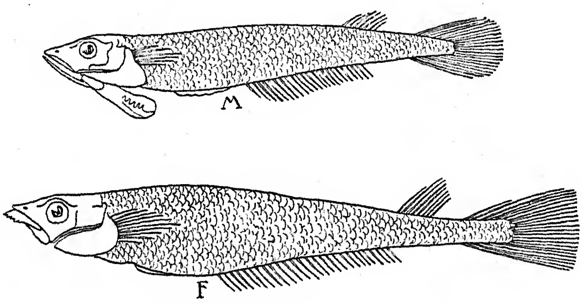


FIG. 68.

Sex Dimorphism in a Small Fish (*Phallostethus dunckeri*). After Tate Regan. The smaller male (M) carries a relatively large clasping organ, situated anteriorly. It is, naturally, undeveloped in the larger female (F).

extra something which the female does not possess in a developed state, if at all. It is important therefore to recall two or three examples of the converse. The females of the frog genus *Nototrema* have a pocket on the back into which the male pushes the eggs. So far as we know, the marsupium or pouch of Marsupials is never more than a rudiment in the males. In the Red-necked Phalarope the female is the more decorative bird.

After a survey of sex-characters, it is well to remind ourselves that conspicuous difference between the sexes is the exception, and general similarity the rule. In many of the higher animals the males and females are very like one another in external appearance. Cat, mouse, rabbit, and hare may be mentioned among mammals; rooks, kingfishers, and many parrots among birds. Below the level of crustaceans, in animals like starfishes and sea-urchins, marine worms, threadworms, jellyfish, and corals, it is rare to find more than hints of sex-dimorphism.

Contrariwise, although there may not be any marked dimorphism, there may be a profound functional difference. There are many facts, long since outlined in our *Evolution of Sex* (1889), which go to show that in their metabolism the male and the female are very different. They run at different physiological rates; the metabolism of the male is relatively more intense. The ratio of katabolism to anabolism is greater in the male than in the female. We may quote a few sentences from another biologist who takes the same view. In his *Sex Antagonism* (1913) Mr. Walter Heape writes: "The Male and the Female individual may be compared in various ways with the spermatozoon and ovum. The Male is active and roaming, he hunts for his partner and is an expender of energy; the Female is passive, sedentary, one who waits for her partner and is a conserver of energy."

Perhaps the average differences between the sexes may be summed up tentatively in this tabular contrast:

Male.	Female.
Sperm-producer	Egg-producer
With less expensive reproduction	With much more expensive reproduction
More intense metabolism	Less intense metabolism
Relatively more katabolic	Relatively more anabolic
Often with shorter life	Often with longer life
Often smaller	Often larger
Often more brilliantly coloured and more decorative	Often quieter in colour and plainer in decoration
Rising to more intense outbursts of energy	Capable of more patient endurance
More impetuous and experimental	More persistent and conservative
More divergent from the youthful type	Nearer the youthful type
Often more variable	Often less variable
Making more of sex-gratification	Making more of the family

THEORIES OF SEX-DIMORPHISM

DARWIN'S THEORY.—As everyone knows, Darwin argued that the evolution of dimorphic sex-characters might be accounted for in terms of selection—especially Sexual Selection. This has two modes: the combats between rival males and the preferential mating where the female chooses or seems to choose. We shall rediscuss this theory in connection with evolution, and so here simply indicate at present that there are some serious difficulties in its way. (*a*) What is known experimentally in regard to selective breeding, e.g. Johannsen's work, does not favour the view that the

level of differentiation of, say, the stag's antlers and the decorations of the Bird of Paradise, could be gradually raised generation after generation by such selection as combats and preferential mating respectively afford. (*b*) In some cases of pronounced sex-dimorphism there is no evidence either of preferential mating or of combats, and subsidiary hypotheses have to be invoked. Thus we have Günther's suggestion that masculine characters have their justification as a means of "bluffing" enemies. (*c*) Statements in regard to serious disproportion in the number of the two sexes must be taken critically, having broken down in several cases. And it is plain that the value of the selectionist interpretation depends largely on the evidence that considerable numbers of the less attractive or less well-equipped males are either left unmated, or have less numerous

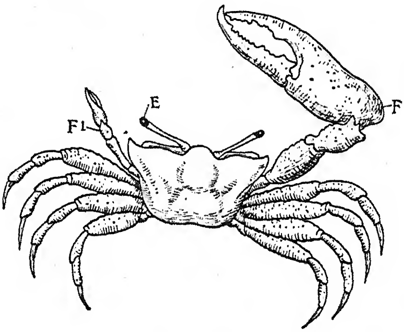


FIG. 69.

The Male Calling Crab or Fiddler Crab (Gelasimus). From a specimen. The male is marked by the exaggerated great claw or forceps (F), which may be as big as the rest of the body. The corresponding appendage, F1, to the left, is small. The male brandishes his brightly coloured forceps when courting the female. The eyes (E) are on long stalks. The four pairs of walking-legs are as usual.

and successful families as the result of their matings. (*d*) As Darwin himself hinted, there is much reason to think that the female who has to be wooed surrenders herself not to the male who has a particular character in special excellence, but to the one whose *tout ensemble* has most successfully excited her sexual interest.

CUNNINGHAM'S THEORY.—In his interesting *Sexual Dimorphism* Mr. J. T. Cunningham argues in support of a Lamarckian interpretation. "In either sex unisexual characters have, as a general rule, some function or importance in the special habits or conditions of life of the sex in which they occur." "But the important truth, which appears to have been generally overlooked, is that in the case of each special organ its special employment subjects it to special, usually mechanical, irritation or stimulation, to which other organs of the body are not subjected. Every naturalist and every physio-

logist admits that in the individual any irritation or stimulation regularly repeated produces some definite physiological effect, some local and special change of tissue in the way of either growth or absorption, enlargement or decrease, or change of shape. Thus not only hypothetically at some former time, but actually at present in every individual, the unisexual organs or appendages are subjected in their functional activity to special strains, contacts, and pressures, that is, to stimulation, which must and does have some physiological effect on their development and mode of growth." To explain the restriction of sex-characters to one sex, to the period of maturity, and often to one period of the year, Cunningham supposes that "heredity causes the development of acquired characters for the

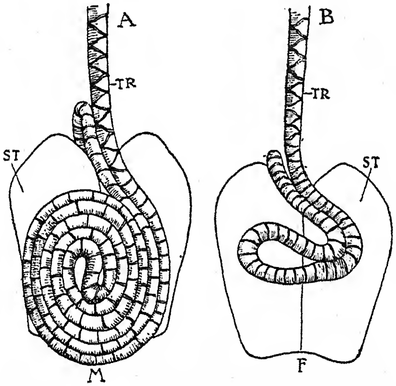


FIG. 70.

Sex Dimorphism illustrated by the Trachea (TR) or Windpipe in the Male (M) and Female (F) of a Bird of Paradise (*Phonygammus gouldi*) The trachea grows down into the breastbone or sternum (ST), and is coiled many times in the male (A), but only slightly in the female (B). After Pavesi.

most part only in that period of life and in that class of individuals in which they were originally acquired". Unisexual characters are largely of the nature of excrescences which originated from mechanical or other irritation in the male or the female at particular times and in particular states of body. They are now part and parcel of the inheritance, but they are not expressed in the body except in association with physiological conditions the same as those under which they were originally produced.

Cunningham seeks to show that sex-characters may be interpreted as the hereditary outcome of special irritations. The legitimacy of this interpretation depends (1) on the experimental evidence that can be adduced to show the origin of callosities, excrescences, proliferations, etc., as the direct result of stimulation, and (2) on the case that can be made out, on experimental or logical grounds,

for believing that somatic modifications may be directly transmitted, in some degree at least. This raises the whole question of the transmission of somatic modifications, which we waive. We simply express our opinion, argued for elsewhere, that the evidence does not warrant an acceptance of Cunningham's theory.

SURPLUSAGE THEORY.—Hesse and Doflein have made the interesting suggestion that as reproduction is very much less expensive in the males, they have surplus material at their disposal which may account for their frequently greater variability, for certain characteristics of habit and temperament, and for their exuberant growths of various sorts.

To the objection that the male is often much smaller than the female, and that his nutritive income will be proportionally less, the answer is given that the decisive fact is one of ratio, e.g. between the amount of material expended in reproduction and the weight of the body in the two sexes, or between the size of the reproductive organs and the size of the body in the two sexes.

In cases where the sexes expend approximately equal amounts of material in reproduction, almost no sex differences occur. Thus in many fishes, such as the herring, the ovaries and testes are about the same size and enormous quantities of milt are shed by the males in the water. In the viviparous Cyprinodonts, on the other hand, where there is internal fertilisation and economy of sperm-material, the males show both permanent and periodic distinguishing features.

In his critique of the surplusage theory, Kammerer indicates some serious, and indeed fatal, objections. (*a*) It may explain how the male has a good deal to spend on decoration, but it sheds no light on the specific line that his expenditure takes—a mane for the lion and antlers for the stag. (*b*) It is easy to pick out cases that suit the theory, but what of the broad fact that in hundreds of cases among birds and mammals, reptiles and insects, the two sexes are equal in size, equal in numbers, and uniform in appearance, although the expenditure on the male's side is very much less than that of the female? (*c*) The female reproduction is physiologically more expensive, but yet it is the female that tends to fatten. And why is it that when her reproductive expenditure is over, her accessory sex-characters do not improve (except in rare cases), but become less marked than ever? (*d*) There are many cases where the male has to fertilise the eggs of many females, and where he has no masculine peculiarities, which is what the theory would suggest. But there are also many cases of a similar sort, where the polygamous male, like peacock, pheasant, stag, bull, sea-lion, shows an exuberance of masculine features. Indeed, it has been suggested that increased sexual function in the male tends to increase the masculine features, and vice versa.

THE RÔLE OF INTERNAL SECRETIONS.—It has long been recognised that the reproductive organs exert a pervasive influence on the body, as is conspicuously seen in the changes that occur at adolescence and in pregnancy even in remote parts of the body. The fact is expressed in Helmont's aphorism: "Propter solum uterum mulier est, quod est", which Chereau changed into "Propter solum ovarium mulier est, quod est".

The view of Pflüger that the gonads exert an influence through the nerves associated with them has given place to the view, originating with Brown-Sequard, that the influence passes into the body by the medium of the internal secretions of the gonads. To Starling we owe the convenient term "hormones" for the specific stimulating substances in these internal secretions.

It may be recalled that a male organ or testis in a higher animal consists (1) of sperm-making cells arranged in tubules, (2) of interstitial cells of various types, and (3) of a connective-tissue outer envelope. Similarly the female organ or ovary consists: (1) of ova disposed in groups or follicles; (2) of interstitial cells of various kinds (the stroma of the ovary, the follicle cells, and the corpus luteum), and (3) of a connective-tissue outer envelope.

It has been shown by many investigators that the interstitial cells of the Mammalian testis possess a relative independence of the germinal portion. They may be well developed at a time when the germinal part is still embryonic; they may occur at some distance from the seminiferous tubules; they may be normal in old testes from which the sex-elements have disappeared, or in diseased testes in which only the seminiferous part is affected. Three functions have been assigned to the secretion of these remarkable glandular cells, that it is nutritive for the testis, that it acts as a formative stimulus for the secondary sex-characters, and that it affects genital excitement.

It has been shown that masculine characters (e.g. in the horse and in man) may develop although the sperm-making part of the testis is degenerate, provided the interstitial part is well developed. It follows that the stimulating internal secretion, without which the masculine characters do not develop, is produced by the interstitial tissue. It has been shown (e.g. in mole, marmot, man) that the interstitial tissue waxes and wanes, and that the recurrence of "heat" in animals is preceded by activity of the interstitial tissue before sperm-making activity sets in. Similarly in the female the internal secretions that pass from the ovary have their origin not in the germinal but in the interstitial part of the organ.

Let us consider the case of fowls. For three or four weeks after hatching, chickens do not show any external marks of sex. In size and colour of comb, in plumage and limbs, pullets and cockerels are alike, and it is not till towards the thirtieth day that the external

differentiation begins to be apparent. By the forty-fifth day the comb is more pronounced and more vividly coloured in the male; the wattles begin to develop; the young cocks crow in the second month; differences in the plumage begin to differentiate the two sexes more and more sharply.

So far we are on familiar ground, and it is also well known that the removal of the testes hinders the development of the secondary sex-characters. But an investigation by J. des Cilleuls (1912) has made matters more precise. He has shown that the appearance of the secondary sex-characters in the young cock coincides with the appearance of interstitial cells in the testes; that the interstitial cells and the distinctively cock-characters increase *pari passu*; and that the cock-characters continue to be accentuated till after the sixtieth day, while the essential part of the testes—the seminal tubules—remains embryonic. It would appear, therefore, that the internal secretion of the interstitial cells serves as a stimulus for the development of the secondary sex-characters.

As Steinach and Kammerer have put it, the changes that occur in the body when an animal becomes sexually mature are conditioned by the internal secretion of the gonads, probably of the interstitial tissue alone. The brain is influenced profoundly, it is "eroticised"; it becomes susceptible to the attractions of the other sex. The cerebral ganglia acquire a tendency to lower the tonus of certain inhibiting centres in the spinal cord, and at the same time the excitability of certain sympathetic ganglia is increased, so that they react to peripheral stimulation.

"The eroticising of the central nervous system also brings about far-reaching changes in metabolism, such as increased blood-supply to the genital and extra-genital sex-characters, which react to this with vigorous, often annually renewed growth, and at the time of puberty reach their full development". In these words Kammerer expresses a conclusion based on experiment and of the highest importance. The gonads by their hormones influence the whole body and in particular the sex-characters, but the influence comes under the regulation of the central nervous system. Yet it cannot be concluded that the secretion of the gonads causes the sex-characters, though it is a condition of their development in the individual. The gonads are the nurses of sex-characters, but not their producers. The characters are in the hereditary treasure-box, even though they are never exhibited. The internal secretion is a condition of their normal development; that is all that can be said.

According to Tandler the criterion of a sex-character is that it reacts to gonadial secretions in a particularly definite way. The gonadial secretions punctuate the growth of the long bones and thus affect the proportions of the body; they also influence the nervous system and the general metabolism; they work in harmony with

other internal secretions. But it is indisputable that they exert a particularly strong and definite formative influence on certain parts —and these are the sex-characters. The difficulty is to understand the history of this correlation.

STATEMENT OF KAMMERER'S CONCLUSIONS.—The first important step in the evolution of sexual reproduction was the specialising of germ-cells as distinguished from body-cells. The second was the differentiation of dissimilar gametes—contrasted in their assimilation capacities, amount of cytoplasm, size, and activity—the microgametes and the macrogametes which unite in fertilisation. The differentiation of sex doubtless occurred very early in phylogeny, and the determination of sex often occurs, as we shall notice later, very early in ontogeny. It is progamic or syngamic; the future sex of the organism is usually quite settled at fertilisation. Before this, during the maturation period, the gametes are probably in varying degrees susceptible to external influence, so that their predisposition or bias to one sex or the other (*eingeschlechtlicher Entwicklungstendenz*) may be changed (it is to be supposed that they all have the primordia of both sexes), but the higher the animal the less is this susceptibility. Only in plants and in the lower animals can we succeed in experimentally changing the progamic predisposition, activating the tendency which should otherwise be latent. The factors that condition maleness ("Mikrogametismus") or femaleness ("Makrogametismus") are ultimately assimilation-differences. Here Kammerer agrees with the thesis of our *Evolution of Sex* (1889).

Removal of the essential gonads changes the metabolism, affects the whole body, and is usually followed by degeneration of the subsidiary and incidental sex-characters. But this cannot be used as a criterion to distinguish sex-characters and body-characters. It seems, in fact, as though the body was "sexed" through and through.

But the castration, however early it may be, never prevents the appearance of the embryonic primordium of any character. The absence of the gonad has a purely quantitative effect on the degree of development which a character may reach, or on the degree of regeneration which may occur after loss. When the essential gonadial substances are introduced in any form (by transplantation, injection, etc.) into a castrated animal, the effects of castration are alleviated or reversed.

Breeding experiments show that sex-characters behave in inheritance like all other specific or racial characters. They illustrate either blended or alternative inheritance. Moreover, hybridising experiments show that indifferent systematic characters may come to be sex-linked, and conversely that the characters of one sex may come to be the common property of both sexes, or may wholly

disappear in the "atavism" that sometimes follows the crossing of widely separated races.

According to Kammerer, sex-characters have arisen phylogenetically, like species-characters, by direct and by functional adaptation. They may have begun in both sexes and have become subsequently specialised in one (usually the male)—and this is probably true, on the average, of the older characters. Or they may have begun in one sex (usually the male) in response to peculiar conditions of life—and this is probably true, on the average, of the later acquisitions.

Sex differences, whether arising directly (environmentally impressed on the passive organism) or indirectly (functionally established by the active organism), become hereditary characters along with the rest of the organisation. What were primarily common to both sexes may be restricted to one; and what were primarily restricted to one may become common to both; and there has probably been a continual flux of sex attributes, the gonadial and genital least, the extra-genital most. So far Kammerer's chief conclusions.

ILLUSTRATIVE FACTS.—Kammerer bases his conclusions, for the most part, on the results of recent experimental work. Let us take a few illustrations from his scholarly survey. The castration of young mammals often leads to a lengthening of the long bones, to a lessening of muscular development, to fattening, to inhibition of brain development, and to suppression of sex-characters such as antlers. The castrated female may show an activation of latent masculine characters, but in the crabs castrated by Sacculina and other crustacean parasites the males put on feminine characters. In certain instances, as Tandler has clearly shown, what is developed after castration tends towards the more primitive condition, to what, in some cases, was probably common to both sexes. A doe with antlers, a bearded woman, and a hen with cock's feathers may illustrate this. In the case of caterpillars, whose sex is determined before they leave the egg, no effect at all is produced by castration. In parasitised male crabs, what happens, according to Geoffrey Smith, is a change of the metabolism to feminine and female lines. In *Inachus* the parasitised male crab develops egg-carrying abdominal limbs like those of a female, and even produces eggs. But in this case the putting on of the external feminine characters *precedes* the appearance of the ovaries.

In some cases, such as the crests of male newts and the swollen "thumb" pads of male frogs, regeneration does not occur unless the gonads are present. In other cases, the regeneration of sex-characters may take place in the absence of the gonads, or in the presence of those of the opposite sex. The influence of the gonads on regrowth is at most quantitative, not qualitative.

The consequences of the loss of reproductive organs can be

lessened or annulled by the implantation of other reproductive organs, which need not be of the same sex, nor inserted in their proper place. The influence is chemical, for injection of gonadial extract is sometimes effective, and in some cases an implanted organ develops only interstitial tissue, but no germ-cells. Extracts of the brain and spinal cord of mammals in heat may produce on castrated animals effects comparable to those that follow the introduction of gonadial material. The influence of the hormones seems to be in great part indirect, through the nervous system.

Not a few experiments, especially on insects, show that changes of environment may affect the expression of the accessory sex-characters, and may indeed change them to those of the opposite sex. An environmentally induced change of metabolism brings about the activation of the normally latent accessory sex-characters of the opposite sex, or (in males especially) prevents the activation of the normal sex-characters. In some cases the gonads are markedly influenced by the environmental change, so that part of the result on the body may be a castration-effect; in other cases the gonads are not affected at all. Kammerer attaches much importance to cases where masculinised females had offspring which were all masculoid—the females as well as the males. He concludes that sex-characters react to the environment just like ordinary somatic characters, and he believes that in both cases there is some measure of transmission of the induced modifications.

SEX-CHARACTERS AND SPECIFIC CHARACTERS.—Tandler and Kammerer have done good service in showing that sex-characters behave like ordinary specific characters, e.g. in inheritance, in regeneration, and in their relation to environmental influence. We think, however, that they have exaggerated a useful idea, so that in its generalised expression it becomes untenable. Tandler says: "All secondary sex-characters were, indeed, at first specific characters . . . and not primarily associated with the genital sphere." Thus the milk-gland has doubtless arisen from a group of skin-glands, common to both sexes. Later on, in the female, it came secondarily into the service of the offspring-nourishing function, and under the influence of the reproductive organs. It is the enigma of its representation in the males that has led to the theory that the mammary gland was originally common to both sexes and not nurtural.

In Bovidæ the possession of horns is a constant character of a given species or variety. They are present in both sexes. The shape-differences between them form the sex-character. When there is early castration in calves of a horned race, the two sexes develop the same kind of horn, which bears a marked resemblance to the ancestral type of *Bos primigenius*.

According to many authorities, antlers began as variations on

the part of the male Cervidæ; they necessarily became part of the inheritance of the females as well; but they could not find expression, so to speak, in the female constitution. According to Tandler, however, they were originally possessed by both sexes, like the horns of cattle, and have in the course of time become sex-linked characters, normally developed in the males only, except in the old-fashioned reindeer, where they occur in both sexes.

Kammerer comes to the same conclusion: "The sex-characters simply form a particular group of species-characters: all sex-characters are at the same time species-characters." At the same time he refers to Möbius's thesis that there is a sort of somatic sex, a sex-differentiation of all the organs and tissues, whether they show a visible difference or not, so that one may, he says, invert the previous sentence and say that all species-characters are also sex-characters. But, in any case, he holds that there are certainly no special sex-characters, which stand apart from other species-characters, as things *per se* and autonomous.

In their important work *Die biologischen Grundlagen der sekundären Geschlechtscharaktere*, 1913, Tandler and Gross are very emphatic in their conclusion that all sex-characters have been derived from specific characters or "systematic" characters, which in the course of time have been brought (by the usual method of variation and selection) into the service of reproduction. This occurred at different periods, as is suggested by their different degrees of variability to-day. And *pari passu* with their evolution they have come into correlation with the gonadial glands of internal secretion which supply their indispensable liberating stimuli. "The secondary sex-characters are to begin with systematic characters and they ultimately owe their development and differentiation to the harmonious co-operation of the glands of internal secretion."

But this thesis that: "All secondary sex-characters were at first specific characters", appears to us to be an exaggeration of a sound idea.

There are, it seems to us, *numerous* peculiarities of one sex or the other which cannot be readily derived from specific characters supposed to be common to both sexes. And if it be said that the cases we would adduce are not fair samples of sex characters, we would reply that it is very difficult to draw a line round "secondary sex-characters", separating them from other sex differences. This is especially difficult among Invertebrate animals, where we have almost no knowledge of glands of internal secretion connected with the essential gonads, and are therefore bereft of that useful criterion of a secondary sex-character which has been discovered in Vertebrates.

Let us consider, then, a few striking sex differences in the light of Tandler's theory. The female Paper-nautilus (Argonauta) is very

different from the male. She is much larger, she has two "arms" peculiarly modified to secrete a unique shell, not homologous with other Cephalopod shells, which is chiefly used as a brood-chamber for the developing ova. The small male has no such shell and no such modification of two of the arms. When he is sexually mature, one of his arms becomes laden with sperm-packets and is discharged as a "hectocotylus" into the mantle cavity of the female.

These are familiar facts, but we do not know of any evidence for supposing that the immediate ancestors of the Paper-nautilus had an external shell or modified arms such as the female now shows. There is no hint of such a thing. Moreover, the shell is not for living

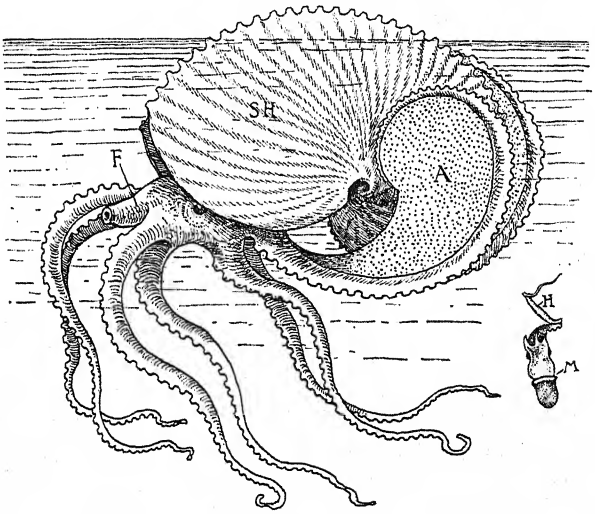


FIG. 71.

Paper-nautilus (Argonauta), the female with the brood-chamber shell (SH), and in proportion the pigmy male (M) with a "hectocotylised" arm (H), laden with sperms. A, one of the "arms" that secretes the delicate shell; F, the locomotor funnel through which water is forcibly expelled. One of the eyes is shown. Most books show the shell upside down.

in, but for the protection of the eggs, it is a cradle not a house, and it has no meaning except in the female.

Again, let us take one of those very interesting cases where the female has something definite and positive which the male has not—the frog *Nototrema* with its dorsal pouch in which the eggs are carried. Is there any warrant for supposing that this was once a specific character?

Another case in point may be found in the so-called claspers of male Selachians and Chimæroids. In a fish like the skate they are very conspicuous sex-characters; they are highly specialised struc-

tures with complicated musculature and skeleton. In the Chimæra they are even more complicated. They are very definitely male organs, and in some cases at least they are inserted into the cloaca of the female in the process of sexual union. Phyletically they are specialised portions of the pelvic fins, but there is no trace of them in the female. So far as we know, there is no warrant for supposing that the ancestors of our modern Selachians had in both sexes structures like the claspers.

Similarly, the male spider is often very markedly distinguished from the female not only in size, but by the great complexity of the

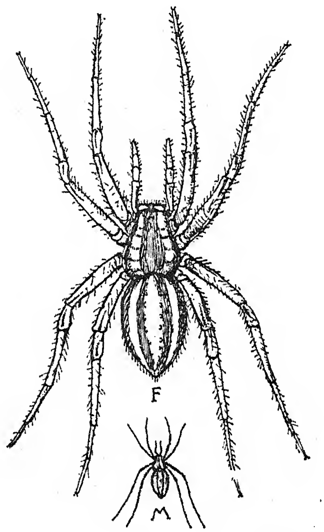


Fig. 72.

Sex Dimorphism in Spiders. Minute male (M) and much larger female (F). After Vinson.

pedipalps which are used in transferring the sperms into the female. The sex-character here is not the pedipalp, which is, of course, common to both sexes, but the extraordinary elaboration of the end of this appendage. We do not know of any warrant for regarding this as other than a purely masculine character.

Again, in most Mammals the testes are carried in an external pouch or scrotum (into which they descend, as if by a normalised rupture, at a certain stage of development), while the ovaries always remain internal. This is a definite male peculiarity, an extra thing that is not hinted at in the female: and we do not know of any warrant for regarding this as a transformation of a specific character once common to the two sexes. In the same way the protruding

egg-sacs of many female water-fleas, e.g. Cyclops, are extra things on the female's part.

MODE OF ORIGIN OF SEX-CHARACTERS.—If we turn aside from the hypothesis that sex-characters arose by the hereditary accumulation of the direct results of somatic modifications, whether functional or environmental, we are led to the view that they arose as germinal variations or mutations. That the germinal origin of variations or of mutations is wrapped in obscurity, makes all phylogenetic ætiology difficult; there is no *special* difficulty in regard to sex-characters; the problem of their origin is probably in essence like that of any other characters.

Without straying far from our present path, we may here state some of the possibilities as regards the origin of variations. (*a*) Fluctuations in the nutritive stream may bring about changes in the germ-cells. (*b*) The opportunities afforded in maturation and fertilisation may bring about a shuffling of the chromosome cards. (*c*) External changes may serve as trigger-pulling variational stimuli to the highly complex germ plasm. (*d*) There is a tendency in matter to complexify, no more explicable than gravitation, but real; perhaps the living unit utilises this in its (*e*) *unconscious germinal experiments in self-expression*, for that is what we believe mutations, at least, to be.

Let us suppose, then, that a germ-cell already predisposed to develop into an ovum-producer was the seat of a variation, say in the determinants or factors corresponding to the future ovary. Let us suppose that this variation was in the direction of producing an accessory yolk-gland. In the course of development the determinant or factor, if consistent with the rest of the constitution, is actualised and there is the beginning of a yolk-gland—an advantageous addition obviously. In the course of time the organism reproduces and its germ-cells have entailed on them (in accordance with the conception of germinal continuity) the determinant or factor of a yolk-gland. But the difficulty immediately arises in the mind that this new hereditary item will be found not only in the germ-cells which will develop into females (where it will be relevant), but also in the germ-cells which will develop into males (where it will be irrelevant). The most obvious difficulty, then, is what will happen to the yolk-gland determinant in those germ-cells that are going to develop into males. The answer is that it will remain latent, not because its expression would be irrelevant, which is a finalistic idea, but because it arose as a variation in a gamete predisposed to develop into a female. It is solidary with femaleness; which, for us, means a metabolism-ratio or rhythm with relatively preponderant anabolism. Metaphorically, it is a seed which will germinate in female soil, which will not germinate in male soil, though it will remain latent there.

For the sake of clearness, let us take the same occurrence on the male side. In a germ-cell (whether ovum or spermatozoon or fertilised ovum) predisposed to develop into a sperm-producer, a variation arises, say, in the direction of brilliant pigmentation of the skin. If it is consistent with the rest of the organisation, it is realised in development; it is a success; all the spermatozoa have the corresponding initiative factor, or gene, and it is transferred to a multitude of ova. But it develops only in those fertilised ova which are going to develop into males. It does so develop because it was to begin with a variation—a new departure—exhibited by a male-producing gamete. It is a seed which can germinate only in a male soil, which will remain latent in a female soil. Thus a germinal variation in those ova of the bee which develop parthenogenetically into drones, will be unexpressed in the queens, but none the less faithfully handed on by them, or rather continued by their egg-cells.

We would, then, suggest the hypothesis, that distinctively masculine characters all arose from variations in gametes predisposed or predetermined to develop into males, that distinctively feminine characters all arose from variations in gametes predisposed or predetermined to develop into females, and that this primal difference in origin explains (1) why the new gains are often confined in their expression to one sex, and (2) why they hang together in a hereditary congeries. The hypothesis is in no wise inconsistent with the view that many sex-characters are transformed species-characters, for the new variation in such cases was the transforming. Nor does the hypothesis conflict in the least with the facts in regard to the importance of hormones in the individual development of the sex-characters, that is a question in the physiology of development. Nor does the hypothesis conflict at all with the view that some process of Selection favoured the persistence and diffusion of the new characters. Nor does the hypothesis conflict at all with the view that the sex-characters behave in inheritance as Mendelian characters. The hypothesis concerns the *origin*, not the ontogenetic development, nor the phylogenetic evolution, nor the mode of inheritance.

One of the arguments that may be used in support of our hypothesis is that used in a slightly different connection in *The Evolution of Sex* (1889). It is this. There are numerous distinctively masculine characters which have some measure of "family resemblance", which look as if they had something in common, which are congruent with the intenser metabolism of the male sex. To a thoroughgoing Lamarckian this is readily intelligible, for he regards the colour-display, the exuberance of integumentary outgrowths, the erection of parts of the body such as crests and tail-feathers, the growth of weapons on the one hand and embracing organs on the other, as natural developments of the intensely living, lusty male, as natural individual developments, whose results have gradually

been incorporated in the heredity-bundle. As we do not maintain that Nature works in this *direct* way, our suggestion is that such measure of congruence as there is in, say, masculine sex-characters (e.g. brighter colouring, exuberant decoration, smaller size) may be hypothetically interpreted as due to their having arisen as germinal variations or mutations in germ-cells predetermined to develop into males.

As a subsidiary hypothesis, we suggest that augmentations of the activity of the gonadial glands (due either to germinal or to nurtural causes) may have from time to time set free in the organism an unusual abundance of hormones with a corresponding exaggeration of individual sex-characters. To those who are Weismannists by conviction, yet having a suspicion that there must be something in Lamarckism after all, we suggest for critical consideration the hypothesis that this unusual abundance of hormones (of the nature of which very little is known) may exert an influence on the germ-cells in the gonads and stimulate in them the determinants corresponding to the secondary sex-characters which are being especially stimulated in the parental body in question.

SEX-CHARACTERS IN INDIVIDUAL DEVELOPMENT.—We can imagine that what obtains in ontogeny is somewhat as follows. The fertilised egg-cell, in a way inconceivable to us, is the vehicle of the determinants (or factors, initiatives, potentialities or genes!) of all the characters proper to the species. It also contains the possibility of giving rise to the characters peculiar to either sex, whether of the essential sex organs, or of the subsidiary sex organs, or of distant parts of the body. It is probable that whatever determines whether the fertilised egg is to develop into a sperm-producer or an egg-producer determines at the same time that it shall develop the masculine or the feminine set of characters. The cause which determines that the fertilised ovum is going to develop into a deer with testes, also determines that it is going to develop into a deer with antlers.

We may compare the determinants of sex-characters to seeds which will not germinate except in particular kinds of soil. The determination of sex settles the question of (protoplasmic) soil. If the fertilised egg is going to develop into a male, all the "masculine seeds" will germinate; if the fertilised egg is going to develop into a female all the "feminine seeds" will germinate. If the sex is imperfectly differentiated, as in casual hermaphrodites, then some "seeds" of both sets—masculine and feminine—may germinate in the peculiar soil. It is easy to read "gene" for "seed", "develop" for "germinate", and "cytoplasm" for "soil".

To the question why the fact that the fertilised ovum is going to develop into a male (or a female) should *ipso facto* imply that all the masculine (or the feminine) characters are to find expression

we have given the answer that the characters are all correlated, they are there or not there *en bloc*, they form a sex-linked assemblance. And as a reason for this correlation we have suggested (1) that all masculine (or feminine) characters originally arose as germinal variations in gametes predisposed to develop into males (or females), and (2) that in some cases these variations may be plausibly interpreted as congruent or solidary with the characteristic male (or female) diathesis. And to this there requires to be added the very important consideration that just as a thyroid gland and a pituitary gland have arisen in the course of evolution with fundamentally important functions in the internal economy of the organism, so in the course of evolution the gonadial glands have arisen, whose internal secretions, working in harmony with other internal secretions, serve as the liberating stimuli and indirectly as the regulators of the development of the sex-characters.

An Illustration: Winged and Wingless Greenflies.—Some greenflies or Aphids give origin parthenogenetically to winged and wingless progeny in varying proportions. It can hardly be doubted that the capacity for having wings is part of the normal inheritance, and that the winglessness is what may be called a minus variation, like the absence of horns in a horned race of cattle, or the absence of a tail in a kitten, or the absence of hair on a child. Some Mendelians would say that the winglessness is due to the loss of a particular hereditary factor or gene (or group of genes). In the lineage or in the maturation of some of the ova the hereditary representative of wings may be lost. This is the kind of interpretation that is usually given of such a condition as albinism, where there has been a loss of the factor or factors for pigmentation.

But Mr. Lloyd Ackerman, who has been studying the grain Aphid (*Rhopalosiphon prunifoliæ*), indicates another kind of interpretation. Perhaps what inhibits the development of wings is a variation in the general physiology of the organism. In the hæmolymph, which corresponds to blood in insects, there are two kinds of fat or lipoid globules, and two kinds of pigmented globules—green and brown. The brown globules are delicate unstable structures which are readily disrupted, and the wing production appears to be dependent on their breaking down. The instability of the Aphid as regards wings appears to be due to the instability of the brown globules. Other features accompany the winglessness, such as peculiarities in size, colour, markings, sensitiveness, as well as the solidification of the fat globules. But the general idea is important that a *biochemical change may greatly influence the developmental expression of the inheritance.*

THE MANOILOV TEST FOR SEX.—Some interesting chemical tests for sex have been proposed by Manoilov and by others. The

addition of certain chemical reagents to the blood or to the expressed extracts of various kinds of organisms has for its final result a certain colour for the male and another colour for the female. In short, the sex can be told from the colour in the test-tube containing the blood, or extract, or even sap. Now the difficulty has been that while some experimenters, such as Manoilov and his collaborators, are extraordinarily successful in applying this test for sex, others get conspicuously discrepant results. Thus half a dozen determinations may prove quite correct, while in the next half-dozen three are right and three are wrong.

A recent investigation by Professor Oscar Riddle and Dr. Warren H. Reinhart has led to a suggestion which seems to us very shrewd. The suggestion is that the colour difference is primarily an index of the rate or intensity of the metabolism. Thus blood from younger birds, with a high basal metabolism (i.e. routine of essential vital

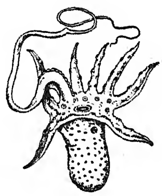


FIG. 73.

The Pigmy Male of the Paper-nautilus (*Argonauta argo*). It differs very markedly from the female not only in being very small, but in having no shell. The figure shows one of the arms transformed ("hectocotylised") as a vehicle for the sperm-packets or spermatophores.

processes), gives a lighter colour than blood from older birds. Aqueous extracts of active tissues (muscle, heart, gizzard) in doves yield a colour lighter than that given by tissues presumably less active, such as those of the liver. The glands of the bird's oviduct yield a lighter colour when actively secreting, and a deeper colour the further they are removed from active functioning. Similarly extracts of whole embryos give the lightest colour when prepared from freshly killed embryos; but decidedly darker when prepared from embryos which have been dead for one to three days. Thus the reason for the discrepancies in previous experiments, in which we have shared, may be that the physiological state, in particular the metabolic intensity, varies notably from one individual to another and at different ages and seasons.

This fits in well with the metabolic theory of sex first stated by us in 1889, in *The Evolution of Sex.* According to this theory, the ratio of Anabolism (constructive processes) to Katabolism (down-breaking processes) is always relatively greater in the females. In the male constitution there is a relative predominance

of katabolism. That is to say, the ratio $A:K$ in the female is fundamentally greater than the ratio $a:k$ in a male of the same weight. It is not, of course, inconsistent with this that there should be, as there often is, a difference in the chromosomes of the nucleus in the two sexes. The chromosomal difference may be an index of a physiological or biochemical difference which goes deeper. It should never be forgotten that one and the same animal may change its sex in the course of its lifetime, and sometimes does so normally —a fact which is distinctly in favour of the physiological interpretation.

But what we are concerned with at present is the suggestion

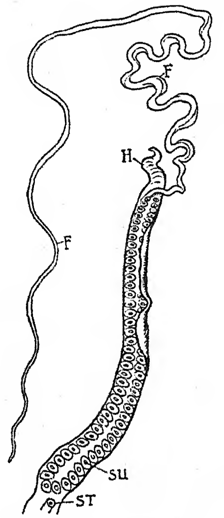


FIG. 74.

The Transformed Hectocotylus Arm of a Male Cuttlefish. ST, the base of the arm; SU, double rows of suckers; H, hook; F, terminal filament.

made by Riddle and Reinhart that the Manoilov reaction is a better indicator of metabolic rate than of sex, and that the reason why it often works correctly in determining the sex from the blood or the extract is to be found in the radical relation between metabolism and sex. "The numerous studies that have been made on plants and animals with the Manoilov test have notably extended the evidence for the metabolic theory of sex."

PARASITIC MALES.—Mr. Tate Regan, Director of the British Museum, has described one of the most extraordinary sex-relationships in the whole animal kingdom—and that is saying a good deal. In three different kinds of deep-water Angler-fishes, two of them new to science, he found that the female was carrying about a

pigmy male (in one case two of them) very intimately attached to her body and dependent on her for sustenance. In two of these strange fishes the blood-vessels of the snout end of the little male were in actual continuity with those of a papilla-like process of the female's skin; and this is the only way in which the male can get any nutriment. The pigmy is an ecto-parasite; and the continuance of the weird association must be due to the fact that it secures the fertilisation of the eggs when these are shed into the sea. The need for the extraordinary inter-relation, which is unique among backboned animals, becomes more intelligible when we notice where these deep-water Anglers live. Unlike their relative, the Common Angler or Fishing-frog (Lophius), which lives as an adult in relatively shallow inshore waters, the Ceratioid Anglers with the parasitic males live in the dark middle depths between 250 and 500

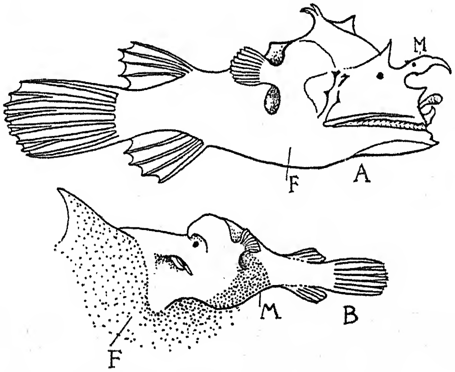


FIG. 75.

Angler-fish (*Photocorynus spiniceps*), showing Male Parasitism. After Tate Regan. A, the female (F) with the pigmy male (M) attached to the front of her head. B, the male (M) enlarged, showing his close attachment to the front of the head of the female (F).

fathoms. They are for practical purposes beyond the light limit, and yet they are not on the deep-sea floor where some other kinds of Angler-fishes have their home. They seem to capture other fishes that are attracted to their luminescent lure, but they do not find life easy. They move slowly in the dark water, and they are few and far between. The fertilisation of the eggs would be precarious, were there not some special adaptation, and thus has arisen the lasting attachment of the pigmy males to the females.

While the state of affairs disclosed by Mr. Tate Regan is unique among Vertebrates, it has some striking parallels among backboneless animals. Long ago, when he was monographing barnacles, Darwin discovered that some of them bore dwarf and degenerate males, which he called "complemental". As they may occur on

hermaphrodites (egg-producing and sperm-producing in one), as well as on female barnacles, Darwin suggested that in the first case the advantage of their presence would be in securing *cross*-fertilisation. In a number of parasitic copepod crustaceans the relatively large female has attached to her body a very minute male; and the fertilisation of the eggs is in this way ensured. For the females are often ensconced in parts of fishes where they are not readily accessible. It is quite possible that the close attachment of a young male to the body of the female is in itself a cause of the inhibition of growth; but this has not been proved for crustaceans. Another

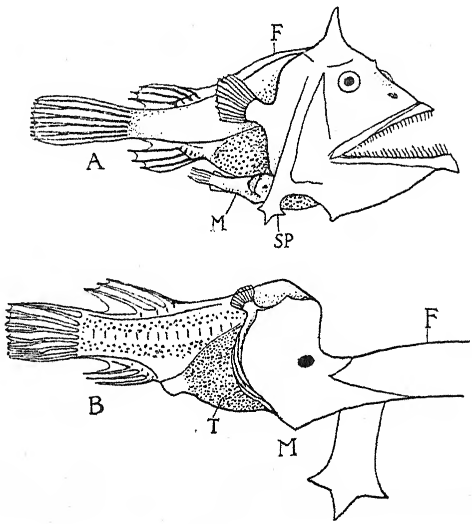


FIG. 76.

Angler-fish (*Edriolychnus schmidti*), showing Male Parasitism. After Tate Regan. A, the female (F) with the minute male (M) attached behind the gill-cover, which is marked by a spine (SP). B, the same enlarged, showing the pigmy male (M), with testes (T), intimately attached to the female (F).

strange case is that of small wormish creatures called Myzostomes, which live fastened to the feathery arms of the beautiful sea-lilies. Some are hermaphrodites and some are females; and here again there are attached pigmy males. While a mother is indispensable, a father may be reduced to a mere appendage, or suppressed altogether! Many of the minute Wheel Animalcules or Rotifers have males less than half the size of the females; and these dwarfs, though free living and sometimes energetic, have not even the honour of fatherhood, since most of the Rotifers illustrate Parthenopeia. In other words, they mainly multiply by virgin birth.

There is no denying that the males or drones among social insects tend to be parasitic, in the sense that they do not fend for them-

selves, but get their food from the resources of the community. The drones of a beehive are not lazy, as is usually believed; they fly about in the precincts of the hive with great energy and great expectations. Functionally, one of them is essential to inseminate the queen on her nuptial flight—the fertilised eggs developing into queens and workers, the unfertilised developing into drones. But if we consider these drones—with mothers but no fathers—from the social point of view, they are parasites. They do not work for their living, but depend on the food the workers gather.

In the first of Mr. Tate Regan's Ceratioid Anglers, a fish from the Arctic Ocean, two small males were attached to the belly of the female, and the Danish naturalist Sæmundsson, who noticed them first, not unnaturally thought they were young ones. The female was about eight inches long; the male about two and half inches. In the second case, from the Gulf of Panama, the female, about two and a half inches long, bore a pigmy male, under half an inch in length, on the top of her head, which seems a strange location. In the third case, from the Western Atlantic, the female carried a pigmy husband below her gill cover.

The British Museum expert seems to attribute the dwarfness to the parasitism, but perhaps it is easier to start with the occurrence of dwarf males, such as occur in not a few fishes. If such a dwarf, much handicapped in the struggle for existence, fastened in its youth on to a female, there would probably be an individual arrestment of growth. Variations in the direction of economy, such as a much-reduced food canal and a suppression of the lure and the teeth, would be favoured in the course of natural selection. We suggest that the dwarfing was not the secondary result of the parasitism, but rather its primary cause.

The Story of Bonellia.—This is one of the strangest of biological stories, profoundly suggestive in more ways than one. Bonellia is a peculiar worm, not uncommon in the Mediterranean, and occasionally occurring in the North Sea. The best known species, *Bonellia viridis*, is marked by a fine green colour, due to a pigment called bonellein. The female has a body about the size of a prune, and this is ensconced in a hole in a rock or among stones. From the mouth there extends a long string-like proboscis, which may be as much as two feet in length and divides into two at the free end. It is used for probing about in search of food, and is very contractile. But while the female Bonellia is conspicuous enough, the male is hard to find. For he is microscopic, and lives in what may be called the reproductive duct of the female. This is an extraordinary case of sex-dimorphism and also of sex-parasitism. The pigmy male has no mouth and must absorb such food as it needs through its ciliated surface.

In 1914, Dr. H. Baltzer, a Swiss zoologist, discovered another

remarkable fact in regard to Bonellia. Out of the eggs there emerge minute free-swimming larvæ, which are at first all alike. After a short time some of them sink on to the substratum, and these develop into the large females. But others, which settle down on the proboscis of an adult female, begin to absorb from the skin, and suffer an arrest of development. They develop into the pigmy males.

Using an ingenious device of staining the cells of the proboscis without killing them, Baltzer was able to prove that the young males absorbed nutritive material from the skin of the adult female. Sometimes he shook off the young males before they had been sedentary for more than a short time on the proboscis of the female, and these developed into strange inter-sex forms, intermediate between males and females. In short, it was proved conclusively that the larvæ which settle down in freedom develop into females, whereas those that settle down in parasitism develop into males of microscopic dimensions and with most of the organs in an arrested state.

At a certain stage the minute young males leave the proboscis and go into the mouth of their bearer. There they undergo a final change. They then emerge and enter the reproductive duct, where they remain for the rest of their life, fertilising the eggs before these are set free.

But Baltzer has been able to take another step of much interest. He has made an extract of the proboscis and finds that it has a poisoning effect on small animals such as Slipper Animalcules, threadworms, small crustaceans, and tadpoles. In very weak solutions it exerts a marked deteriorative effect on the young pigmy males, and a concentration of one part in three thousand is rapidly fatal. An extract of the wall of the female's reproductive duct, in which the parasitic male takes up its abode, is not injurious, therefore it seems practically certain that the arrest of development experienced by the larvæ on the proboscis is due to the absorption of some specific substance from the female's skin. The only step awanting is to treat the free-swimming larvæ with very weak solution of the extract. It should make them all males!

To sum up: Baltzer concluded that the minute free-swimming larvæ of Bonellia are at first all alike; that some settle down on the substratum and develop into large females; that others settle on the proboscis of a full-grown female and, absorbing a secretion of the superficial cells, suffer arrest of development, and become pigmy males. If the sojourn on the proboscis of the adult is artificially shortened by shaking the larvæ off, they develop into inter-sex forms. It was shown experimentally that an extract of the proboscis skin has a deteriorative effect on various small organisms. All this is strongly suggestive of the conclusion that the primary difference

between male and female is physiological, depending on some radical difference in metabolism.

But another way of looking at the case has been suggested by Goldschmidt. He regards the influence of the proboscis secretion as stimulating precocious sexual differentiation, whereas Baltzer thought more of the retardation of development. Moreover, Goldschmidt suggests that there are from the start male larvæ and female larvæ. Those larvæ that have the Mendelian factor for femaleness will always develop into females. Those that have the Mendelian factor for maleness will usually become males if they settle on adults. But if the settling down lasts for a short time only, the larvæ will become inter-sexes. And if the parasitic stage is skipped altogether, the larvæ with the male determinant will develop through transitory inter-sexuality into female forms. It may be, then, that some revision of Baltzer's interpretation will be required in the light of Goldschmidt's suggestions.

COURTSHIP AMONG ANIMALS

What may without any very appreciable metaphor be called animal courtship is as diverse in its expressions as there is manifoldness in individuality. We must not think of the courting creature as thinking out a programme, or meditating on its music, or planning an attractive and ceremonial approach, as might be true of human kind. It is rather that the animal is full of passion and desire, and lets itself go, in an abandonment of self-expression, along lines which are prescribed by its inborn instinctive equipment: and these lines, whether of song or dance, of display or tournament, it may be of luminescence or fragrance, have been sifted out—in the course of millennia—as those that proved most effective in awakening interest and admiration, sex-excitement, and the sympathetic resonance of passion in the desired mate. No doubt there are individual variations, as in the song of the nightingale and the lark, but the main lines are prescribed by the hereditary endowment. Little improvements are always being added, especially when the males are in the majority; which, unless polyandry supervenes, is generally a good thing for the race, since it leads to a higher valuation of the females. In the vast majority of cases, it is, of course, the male who does most of the wooing; but there are quaint exceptions that give us pause. Such are the Grey Phalaropes, which breed in the Far North and pass our shores or linger on them in autumn. For in this attractive bird, the female does the courting, and the male the brooding.

Naturalists, like other fallible men, are often apt to take over-simple views of familiar occurrences; and some are quite satisfied

with saying that the significance of animal courtship is to attract the attention and awaken the passion of the desired mate. But the courting ceremonial is often so extraordinarily elaborate and prolonged—almost like a ritual—that we feel bound to agree with W. H. Hudson and Julian Huxley that it has in these cases a deeper than physiological significance. It forges psychical bonds which keep the mates loyal partners and devoted parents when the storm of passion is past. Controlled courtship may raise fondness into love; and this unconscious end is its higher evolutionary significance.

We miss part of the meaning of courtship if we do not appreciate the elaborateness to which it may attain. Thus Julian Huxley's study of the Great Crested Grebe has shown that for this bird the courtship includes waggling and swaying, bending and shaking, a "cat-attitude" of display, a "ghost-dive", and an offering of water-weed gifts! The ceremonies establish emotional bonds. Even in one of the most familiar of birds, namely, the lapwing or peewit, there is intricacy of courting behaviour—the extraordinary aërial dance of the males, with its nose-dives and somersaults, the prayerful cries, the "wing-music", the posing and the show-off, and the excited formation of suggestive "scrapes" in the ground. The male Frigate Bird has an incredible inflatable scarlet throat-pouch, and here is Mr. Beebe's description of his behaviour: "Another emotion obsessed him; he bent his head back until it sank between his shoulders, the red balloon projecting straight upward, and the long angular wings spread flat over the surrounding bushes. The entire body rolled from side to side, as in an agony, while the apparently dying bird gave vent to a remarkably sweet series of notes, as liquid as the distant cry of a loon, as resonant as that of an owl. In our human, inadequate verbal vocality, I can only record it as kew-kew-kew-kew-kew-kew. In a higher tone the female answered him from the sky, oo-oo-oo-oo-oo-oo."

When we pass from birds to mammals we have to admit a rather poor second. For there may be no courtship at all; and when it has been evolved, it is on the side of vigour rather than of art. It is true that there are sometimes passionate sex-calls, of which we have knowledge in the cacophonous caterwauling of the cats on the roof; but these seem a sad bathos after the lyrics of the birds. There are weird howlings among monkeys and powerful bellowings among deer, but they are not very artistic! Fondling and kissing are well-known, especially in the wiser mammals, such as elephants: occasionally there is a display of agility, as in the antics of the March hare. In some cases the males have special decorations which are shown off at the courting time, as when the Elephant Seal inflates the big hood above his snout. It may also be that the fierce combats between rival males, well known in stags, antelopes, and sea-lions, may sometimes serve to excite the females if they stand

by as spectators. But the victorious bully does not seem to give them much choice. On the whole we must confess that there is not much to boast of in the courtship of mammals; at any rate till man, at his best, rises to lover and to poet.

One must not expect too much from cold-blooded animals; but a few of them have courting activities. The male crocodile curvets and capers in a most undignified way, roaring and bellowing at the same time, and perfuming the water with a copious secretion of musk from the skin-glands of his lower jaw and tail. Mr. W. P. Pycraft, whose *Courtship of Animals* (1913) is a treasure-house and a biological education, once had the good fortune to see a Painted Terrapin flogging his desired mate's head with the whip-like ends of his long finger-nails. Some lizards show off their graceful frills and coloured collars, and one of their attractions is to open the mouth very wide to show the vividly coloured interior. This looks like wooing with a yawn! Some of the male newts go in for amorous writhings and fondlings, as well as display; and we cannot listen to the croaking of the frogs in spring without being reminded that the first use of the voice was as a courting-call.

In most fishes the sexes can hardly be said even to come into contact; but there are cases where the rival males fight, where the male caresses the female, or swims around her excitedly, sometimes flushed with gorgeous colour, as in the Gemmeous Dragonet. But there are a few fishes that strike a subtler note. The male stickleback is dazzling when he puts on his wedding-robes; he challenges rivals and they fight fiercely. A remarkable feature is that the females swim about in troops outside the battle-ground, and now and then the victorious polygamous male selects a temporary mate from the company and induces her to visit the nest that he has built. But the females are not passive. "The female that heads the troop swims forward with rapid darts, followed by the others, suddenly stops, and assumes a vertical position with her head towards the bottom." The others follow suit and take up a similar position. Then the leading female suddenly deals a blow that scatters the crowd, which forms again in a few minutes. What can this mean? In the Rainbow Fish, where the male makes a floating nest of Algoid filaments, and buoys it up with bubbles, there is a courting performance, in the course of which the male brings the female just under the green sunshade, so that when the eggs are liberated they float up and are caught in the bubble-nest.

In the lower reaches of the Animal Kingdom there is often some sort of courtship, if we use the word, as we must, somewhat elastically, to include signals between the sexes and all outward display of sex-desire. In most cases this cruder courtship is so far away from our understanding that we get an impression of "queerness". Nature is sometimes *farouche*. The apparently apathetic snai

presses a beautifully formed arrow of lime at its neighbour—the *spiculum amoris* or Cupid's dart. Luminescent signals pass from the female glow-worm, sitting in the grass, to attract the even more luminous male who dances in the air, and the lady gathers a levee. The male death-watch knocks his head against the wainscot; what is taken by the superstitious as a presage of death being his knocking at the door of his desired mate. The grasshoppers trill merrily, the cicadas "sing" to the breaking-point to their voiceless wives (dull of hearing though they be), the crickets chirp, and there are other forms of instrumental music drawn into the service of Love. The male spider often fights with his rivals, lustily and skilfully, but not to much hurting; he dances round the capriciously tempered female, showing off his good points of colour and agility; he sometimes courts from a safe distance by vibrating a silken thread that leads to the spinster's web.

There is a moral to this brief survey, for is it not one of the encouraging facts of Organic Evolution that fair flowers arise from earthy roots, more useful than beautiful? In the lower levels of animal life there is no wooing at all; imperceptibly there is an evolution of sensory appeals, and the lusty may become the fond; gradually there appear indubitable expressions of emotion and hints of psychical as well as physical tendernesses; the leaves of fondness become the flower of love, whence, may be, the fruits of the spirit. In any case, as Socrates said in speaking of the "religious and human love" of the halcyon, "there is comfort in this, both for men and women, in their relations with each other".

COURTSHIP OF THE ALBATROSS.—In Mr. Beebe's *Arcturus Adventure* (Putnam's, 1926) a graphic account is given of the courtship of the albatross. One walked up to another, who rose and faced him. They stood with their breasts about a foot apart. He suddenly shot his head and neck straight up, the bill skyward, and uttered a deep, grunting moan. She followed suit and then, alternately, each bird bowed deeply and quickly three times. "Without an instant's delay they next crossed bills and, with quick vibratory movements of the head, they fenced—there is absolutely no other word for it—with closed mandibles." Without warning, the male suddenly stopped and again shot his head high up into the air. Whereupon she instantly turned her head and neck far sideways, close to the left wing and side. Then another double bow and a second bout; then a rest for a few minutes, followed by more fencing, the male with widely open mandibles. It is an astonishing ritual, but entirely in keeping with what we are beginning to know in regard to many birds. Mr. Beebe is not the first to describe it; but he does it well, and he got a complete series of motion pictures of the fencing. He bowed to one of the solemn birds, and got it to return his salutation twice. The ceremonies may be repeated even when the birds are

already in possession of an egg, and they are marked by the calmness one would expect from an albatross. There may be grunts and groans or there may be complete silence. There is no emotional climax.

COURTSHIP OF SPIDERS.—For forty years or so it has been well known that the quaint ways of courting spiders deserve inquiry and admiration. They show diversity, intricacy, and abandon to a degree that fills us with scientific curiosity, and sometimes leaves us wondering whether we have more than begun to understand living creatures.

Among the Jumping Spiders, which leap on their victims and are much less shortsighted than most of their kindred, the main method of courtship is the dance. The male is very agile, and he often has special decorations on his front legs or elsewhere; and these he obviously "shows off" in his tireless waltzing before his desired mate. He sometimes circles round her a hundred times, and she becomes more and more interested in his display. A significant feature is that each species has a dance of its own, for this spells individuality.

Among the wolf-spiders, which have also good eyesight, the usual practice of the male is to stand on tiptoe and wave his decorative palps or his forelegs in semaphore fashion; and he does it with quaint seriousness. In his admirable *Biology of Spiders*, Savory tells us of a common British relative of the wolf spiders who has got no decorations to wave, but has hit upon the brilliant idea of presenting wrapped-up flies to the female.

These courtship gifts have their analogues at the human level; but there are some remarkable features. On one occasion a spider suitor with "a frugal mind" was seen offering his desired mate a fly which he had himself previously sucked! She told him emphatically that this sort of thing wasn't done.

The web-weaving spiders are mostly shortsighted, touch counting for much more than vision, so it is not to be expected that they will go in much for dance or display, for these would not be seen. We wish to state the case cautiously, since we are convinced that much of the courting activity is an expression of irrepressible masculine excitement, and might possibly be exhibited though the females did not see at all. Similarly, it is by no means certain that female insects, like katydids, always hear the instrumental music of the serenading males. The fact is that the less we say the better about hearing among insects. Be this as it may, no one will dispute the point that shortsighted spiders will not win their mates by semaphoring from an invisible void. But what an exquisite sense of touch they have! If the male of one of the house-spiders is put on the female's web, he begins at once to drum with his palps on the silken sheet. It is, of course, far from being loud drumming, but

the female is aroused in a peculiar way by her suitor's vibrations, while to others she may be indifferent or react in hostility. She waits expectantly, and in the species we are thinking of (*Agelena labyrinthica*), she falls at his touch into a cataleptic swoon, of which he takes his full advantage. But what impresses one most is the frequent subtlety of the business, as when, in another type, the male pulls the threads of the female's web in a peculiar way, and taps impatiently, now at one angle and then at another, around his desired mate's retreat, delivering, as the French observer says, "une véritable supplication amoureuse". The female responds, and there is a—what shall we say?—telegraphic, or teletactile, courting. After the exchange of sentiments has lasted for half an hour, the female may be induced to come out; and then he takes her by the hand and leads her away. There are many different forms of this tactile signalling, and several are well seen in the family to which our Garden Spider belongs. Here there is the added complexity that the female sometimes puts an abrupt end to the performance by rushing at her suitor and killing him. But this episode has been badly exaggerated, for the cannibalism, which is only occasional, usually means that the male has not been courting properly. If he is too crude in his on-coming, or if he has forgotten to bring a gift, why, he must be punished!

In the *Proceedings* of the Zoological Society for August 1929, Mr. W. S. Bristowe gives a circumstantial account of the mating habits of many British spiders; and one cannot but be impressed by the long gradation from rough-and-ready capture of a mate to elaborate forms of courtship, in which the display or appeal may be visual, tactile, or olfactory, and by signalling from a distance as well as by contact or close proximity.

What is the meaning it all? Part of the answer is doubtless to be found in two facts frequently observed by Mr. Bristowe. The first is that the eager male has to face a female with a strong killing instinct, even keener than his own. In many cases it is part of the spider's organic or hereditary make-up to rush at or leap upon a moving object that suggests a possible meal. Thus as the male approaches the female, usually larger and often much larger than himself, he stands in considerable danger of being killed or injured. But once a male has been "recognised" by a female he is relatively safe. Hence the importance of letting her know as soon as possible who he is. This may be effected by displaying characteristic decorations, or making characteristic movements and vibrations, or by offering a gift, or by exuding a characteristic odour.

The second important fact is that, while the recognising female may let her suitor pass if he behaves himself, she may be so uninterested, or unready or preoccupied that she will not respond to his advances. Hence the value of some form of courtship which may

by its ardent importunity so stimulate the female that she condescends first of all to be interested and then perhaps to reciprocate. Some males will be more successful than others; but Mr. Bristowe doubts whether sexual selection in Darwin's sense can be convincingly proved. It seems to us, however, that his observations afford sufficient basis for Darwin's theory, as it would be re-stated to-day.

There seems to be good sense in the "recognition and excitation" theory; but we must not think of the amorous male spider as an intelligent homunculus, nor of the coy female as "recognising" him in our sense of the word. For both sexes are dominated by hereditary "chain-instincts" which prompt them to follow unthinkingly a certain routine of behaviour. From what we know of spiders we feel bound to say "unthinkingly"; yet we have an open mind as to the degree to which the enregistered behaviour-promptings are suffused with awareness and backed by endeavour. We believe, though we cannot prove, that some awareness and some endeavour accompany most of the complex instincts. They are miles away from intelligence; but in origin and in actuality they are not to be dissected off from mind.

It is well known that some male spiders at the courting-time will fight protracted duels without hurting one another. They stop when they are tired, usually without drawing blood. We agree with Bristowe that these combats have been described too generously, for it is very unlikely that they express rivalry or jealousy or anything very subtle. In all probability they express the excitement of disappointed or frustrated males. A lusty male spider will sometimes fight with his own image in a mirror—a quaintly inverted Narcissism.

What is clearly indicated by the behaviour of courting spiders is the frequent subtlety and specificity of the ways in which the amorous male brings himself to the notice of the female and excites her interest and her sympathy. The probability is that the type of male most successful in this art of courtship will have most success in actual reproduction and parentage, and will thus be favoured by selection—both natural and sexual.

HOWARD'S STUDIES ON SEX-BEHAVIOUR IN BIRDS.—The study of sex-behaviour in birds has been deepened by Eliot Howard's patient and critical observations; and we propose to give a short account of his important *Introduction to the Study of Bird Behaviour* (1929). The characteristic of the book is that it studies the behaviour of birds as living wholes and in their natural environments. "One reaction in itself is neither more nor less important than another; each forms a portion of the environment for others; each is sensitive to the modification of others—they form a con-

stellation, and somewhere in the organisation of the living bird they have a common structural link." "The whole has value, the parts by themselves have none."

Mr. Howard begins with the reproductive behaviour of a reed-bunting, and distinguishes four phases. In the first, the female does not figure as a "situational item", and the male is much occupied with his "territory" or preserve, for example, a certain alder-tree and the ground round about it. In some measure he continues doing what he did before, making excursions to the wonted feeding-ground and meeting his old companions. What is new is his persistent song, his preoccupation with his territory, and his growing hostility towards other males. The old and the new are contrary, yet they persist side by side.

In the second phase, about the middle of March, the female begins to play her part, affecting neighbouring males in diverse ways according to their individual physiological state. She is chased with eagerness, but seems to try to escape; for though she excites others, she is not herself in a condition to breed. The male fights furiously with rivals; he expresses excitement (*a*) by a new rippling note, low and musical; (*b*) by a peculiar kind of slow sex-flight, now butterfly-like and again moth-like; (*c*) by quite peculiar expansions and vibrations of wings and tail. All the time, however, the alder-tree and the rush patch have for him a commanding attractiveness. It is only gradually that they extend their influence through him to the female. For at first she is anything but intrigued by sexual excitement on the part of the attracted male, who sings and postures and pursues; she may indeed fly to another alder and feed with another male, or be chased by several suitors. Gradually, however, as the days pass and her physiological condition changes, she attends to her would-be mate's movements more closely and follows them; she observes his boundaries and becomes attached to the territory; she watches a combat with some excitement; and finally she herself fights against intruders, fights as her mate fights, though less viciously.

The third phase is marked by coition, nest-building, and the laying of eggs. There is a great change in the female's behaviour, for she now pursues her mate, settles near him, extends and rapidly flutters a wing, and harasses him, as he used to harass her, until she is satisfied. This beginning of sexual function apparently synchronises with her first hints of nest-building. These hints are at first very vague and desultory. She breaks off a piece of rush, holds it attentively, flies to the tree, drops it casually, and turns to preen her feathers! A few days later she tears off another piece and lays it in the centre of a clump of rushes near the headquarters of the territory. In a few minutes she does the same for another clump, and then for another! About a fortnight after she plucked the first

piece of rush, her ovary ripens, and she fixes on one of the suggestions of a nest, and begins to build rapidly. She is assisted by the male, who has been watching her, and has also made some independent experiments of his own. Yet even now the female's nest-building is curiously punctuated, for after she has worked hard for a short time, usually in the early part of the day, she turns aside and attends to something else. Two or three days pass before the finer strands are added to the nest and the lining is made. The last of the five eggs is laid 19–22 days after the first attempt to build. The male is still keen about his territory, but he is now for the most part very silent, and sex-excitement is markedly waning both in him and in her. He may even tolerate a rival male on his preserve.

The fourth phase is marked by the common care for nest, eggs, and young. With this the female is entirely preoccupied; for the male it is a new attraction, but one subordinate to the claims of the territory. "He finds food and distributes it amongst the young, broods, cleans the nest, in fact does all that she does, and may do it with even greater energy." Sexual behaviour has disappeared for the time being, but it is interesting to notice that posturing still persists, in the female at least, though the reaction with which it was formerly correlated has disappeared.

The courting bird is moved by constitutional impulses, hereditarily engrained and expressed in a particular sequence, just like other differentiations. The changes in the body as a whole influence the gonads, and these liberate regulative hormones; and the sequence is punctuated by external periodicities of temperature, pressure, humidity, and the like, operating from without inwards. Change of diet is probably in some cases another liberative stimulus, but Mr. Howard does not say much about this.

Let us look back on the four phases, well-marked in the Reed Bunting and the Yellow Bunting and in some other birds which select a "territory".

(1) In the first phase the male behaves in five new ways—seeking an appropriate headquarters or territory, occupying a conspicuous position, indulging in exuberant song, sometimes experimenting with nest-building, and fighting with rivals. He is in a condition to behave sexually if stimulated. (2) In the second phase the female arrives, but she is physiologically unready. The male's song is popularly regarded as evoked by the female's presence; but "instead of singing with renewed vigour, he gives it up and sings but little—perhaps stops". The form of fighting among rivals changes, and the male eagerly chases the female, who seems to enjoy it, though not as yet fully responsive physiologically. (3) In the third phase the female begins to posture or to posture in a new way. She may even take the initiative and incite the male to pairing. This

synchronises with toying with building materials; and changes in the two activities occur simultaneously and are proportionate in intensity. (4) The fourth phase concerns incubation and the care of the young. The female loses susceptibility to sex-stimulation and this reacts discouragingly on her mate. It is difficult to tell what evokes the female's brooding, and the difficulty is not lessened by the fact that she will sometimes brood on an empty nest. What can be said save that brooding is a primary response, rhythmically induced, part of the hereditary pattern, instinctive as many would say, though Howard declines to use the word. When the young are hatched, their note of hunger is a powerful stimulus to the mother, and yet when she brings food to the gaping youngsters, she may swallow it herself!

Soon after the young birds leave the nest the sex-cycle may begin again, but it is a remarkable fact that the influence of the offspring remains upon the male more than upon the female. There appears to be some "secondary physiological control" (requiring further analysis) which operates in the female, but not in the male. Thus, when the new cycle begins, she is finished with the young, and ignores their appeal. In the buntings, they would be lost if it were not for the still persistent *paternal* care. Similarly, at a different period in the cycle, the male Whitethroat builds before he has been found by a hen; and the male Lesser Whitethroat not only builds, but sits upon the nest. The male is ahead of the female in susceptibility to both sexual and parental stimulation.

It seems to be an outstanding fact that the inherited pattern of reactions has unity or combined singleness. The bird is an integrated whole and it behaves as such. How is this unification brought about? An important factor is that any one reaction wanes in the course of prolonged excitation, not by muscular exhaustion or the like, but in some subtler way like "fatigue" in a reflex. This waning lessens the risk of overdoing any one line of activity, say fighting, and tends to effect a harmony of reactions, which makes for the attainment of a common biological end, namely, the production of a brood at an appropriate time. The waning of the reaction leaves the "common path" free for a different reaction, and conflict of reactions is thus avoided or lessened. The waning of a reaction under prolonged excitation is an automatic integrative agency.

Howard has gone further than his precursors in working out a connected story of the successive events in the reproductive behaviour, and in showing how they are co-ordinated towards the end-effect—namely the effective production of a brood. We cannot do more than mention a few instances of this; the fixing on a territory helps towards the subsequent feeding of the young; the conspicuousness of the perch and the vigour of the song attract the visit of a female; her presence stimulates the male and she enjoys the com-

panionship; his experiments in nest-building may arouse her similar activities; the sexual flights may increase intensity of sex-excitement and reaction and make fertilisation eventually more secure; posturing has probably a self-stimulating as well as mate-exciting function; the improvement of the weather as the season advances will intensify the reaction and break down the barrier to fertilisation; even the postponement of a reaction may be pressed into the service of the organism, for it may make for effective timing and intensification. In short, "the actions of male and female combine to form a harmonious whole, beautifully adapted to bring about appropriate synchronisation of rhythms".

The behaviour of birds at the breeding season may be physiologically described as "a neurally linked pattern of reactions for which there is inherited structural provision". This is very much the same as saying that the behaviour is the expression of concatenated reflex actions, hereditarily determined. It must be admitted that these chains of reflexes work very effectively, and they have a marked imperativeness. *Why, then, drag in mind?* If it be answered that the behaviour is so perfect that it is impossible not to credit the bird with intelligent prevision, this common-sense argument from analogy is somewhat countered by simple experiments which show that a slight disturbance of routine may cause the creature to behave in a way that looks exceedingly foolish, as when it broods persistently on nothing. But Mr. Howard finds convincing evidence of mind in the individual bird's establishment of territory. This is a mental edifice reared upon three things—song, hostility, and area. In a certain physiological state a male bird selects a territory that influences or attracts him. From the very first there is a linkage of the bodily excitement and the selected territory; there is heightened perceptor activity and a deep and lasting impression is made upon the bird's organisation. "And this impression is so linked with the pattern of reactions that whenever there is recurrence of the territory situation there is excitation from within of the centres initially stimulated from without and revival in the form of imagery. Hence the trees A, B, D, H, K, S, are not only objective to his mind but are susceptible of revival."

It comes to this, that perception and reference reach a higher level of activity when certain physiological changes are occurring. The bird exercises dominion over his territory, but it also exercises dominion over him. Thus from a distance out of sight, when feeding near his mate or his rivals, he will suddenly make for his tree. There is a revival in the form of imagery whenever there is a return of the bodily commotion which primarily intensified the bird's power of reference. Almost everything the bird does is in reference to his territory; it has a controlling guiding influence; a cognitive reference introduces a prospective factor; and this

prospective factor is not disclosed in the *physiological* part of the story.

Mere sensory stimulation fails to account for the way a male bird behaves to his territory. The physiological story needs to be completed by a psychological story in terms of reference and revival in the form of imagery. *Thus mind integrates the reactions.*

Mr. Howard's book is one of the most important contributions yet made to the study of bird behaviour. His patient and critical observations show that the courtship has an intricacy, subtlety, and individuality greater than we knew; the sequence of the chapters in the sex-story has been made clearer; the importance of recognising the creature as a whole has been corroborated; and the alleged uselessness of the mind has been disproved.

THE DETERMINATION OF SEX

The determination of sex is one of the partially solved problems of Biology. Over and over again the solution has slipped through the fingers of science just when they seemed to be closing upon it. It is peculiarly elusive, perhaps because it is near the central secret of life itself.

From ancient times a keen interest has been taken in the question of the determination of the sex of the offspring. Many of the answers are bound up with "theories of sex", which are legion. There can be no doubt that the number of speculations connected with the nature of sex has not fallen off since Drelincourt, in the eighteenth century, brought together two hundred and sixty-two "groundless hypotheses", and since Blumenbach caustically remarked that nothing was more certain than that Drelincourt's own theory formed the two hundred and sixty third. Subsequent investigators have at least tried to add Blumenbach's theory of a fundamental "Bildungstrieb" or formative impulse to the scrap-heap.

The numerous answers offered to the question: What settles the sex of the offspring? illustrate the progress of inquiry into the facts of nature. As in so many other cases, the problem has been looked at in three different ways. "For the theologian, it was enough to say that 'God made male and female'. In the period of academic metaphysics, still so far from ended, it was natural to refer to 'inherent properties of maleness and femaleness'; and it is still a popular 'explanation' to invoke undefined 'natural tendencies' to account for the production of males or females. Thirdly, it has been recognised that the problem is one for scientific analysis." (Geddes and Thomson, *Evolution of Sex*, 1889; revised edition 1901, p. 35.)

There is a library of books and pamphlets dealing with the determination of sex, but a large number—redolent as they are of

good intentions—must be set aside at once because of *obviously fatal* defects in their scientific procedure. Some lay stress on *unverifiable* factors, such as the desire of the parents or parent to have a male child. Others allege the operation of factors which are physiologically absurd. Others base a generalisation on an outrageously small number of cases.

THE PROBLEM STATED.—The general problem is: What determines whether a fertilised egg-cell will develop into a male or a female organism? But let us look at particular forms of the problem. What are called "true twins" in the human race arise from the division of a single ovum into two independently-developing ova, and they are said to be always of the same sex—identical in this as in their other features. But ordinary twins, which arise from two distinct ova developing simultaneously, are often of different sexes. Why is there this difference?

In one household the family consists of boys and girls, in a second of boys only, in a third of girls only. What determines this?

The unfertilised eggs of a queen-bee develop into drones, while the unfertilised eggs of Aphides (produced all through the summer months) develop into parthenogenetic females, until the end of the season, in autumn, when males are produced. What does this mean?

A step would be gained if we could narrow the issue by answering the question, *When* is the sex of the offspring finally determined? How long may a germ-cell remain with the potentiality of either sex? Is there sex-determination before fertilisation or during fertilisation, or not until after fertilisation?

Prof. V. Haecker has proposed a useful terminology. Sex-differentiation implies that one of the two sex-primordia in the germ-cell is activated, while the other remains latent; or, to put it more cautiously, one of two lines of development (towards maleness or towards femaleness) is in some way determined.

(*a*) This may occur before fertilisation—*progamic* sex-differentiation—as in the large and small ova of Dinophilus, Rotifers, and Phylloxera.

(*b*) Or it may occur at the moment of fertilisation—*syngamic* sex-differentiation—as in the case of the hive-bee, where the fertilised ova become females (queens and workers) and the unfertilised ova males or drones.

(*c*) Or it may (theoretically) occur after fertilisation at some stage in development—*epigamic* sex-differentiation. Of the last, however, no convincing case is at present certain.

DIFFERENT WAYS OF ATTACKING THE PROBLEM.—The problem of the determination of sex has been attacked scientifically

along three distinct lines, which are complementary, not opposed. In some cases there has been a combination of two methods.

Statistical.—Some conclusions as to the determination of the sex of the offspring have been based on statistics, e.g. of the relative numbers of male and female offspring in different localities, at different times, with different ages of parents, and so on.

Cytological.—Some conclusions as to the determination of the sex of the offspring have been based on observations of the germ-cells in particular cases. Thus it has been shown that some animals have two kinds of ova, the larger developing into females. In quite a number of animals there is dimorphism of spermatozoa.

Experimental.—Some conclusions as to the determination of the sex of the offspring have been based on experiment, e.g. subjecting the eggs, or the embryos, or the parents to peculiar conditions of nutrition, temperature, and the like, and observing whether the numerical proportion of the sexes in the offspring is in any way different from those obtaining in ordinary conditions; or by contrasting the results of fertilising immature and over-ripe ova; or by trying particular breeding experiments in reference to what are called sex-limited characters.

CLASSIFICATION OF THE THEORIES.—There are two main alternatives: 1. Are there two different kinds of germ-cells (male-producing and female-producing), which are, in their occurrence and in their development, quite unaffected by environmental influence? or, 2. Do environmental influences give the germ-cell, either in its early stages or during its development, a bias towards becoming a male or becoming a female?

But a more detailed classification may be clearer and more convenient for discussion. Five theories may be distinguished.

(*a*) That environmental influences, operating on the sexually undetermined offspring (after fertilisation), may have at least a share in determining the sex.

(*b*) That the sex is undetermined until the germ-cells unite in fertilisation, when it is decided by their relative condition, or by a balancing of the tendencies they bear, neither sperm nor ovum being necessarily decisive.

(*c*) That the sex is fixed at a very early stage by the constitution of the germ-cells as such, there being female-producing and male-producing germ-cells, predetermined from the beginning and arising independently of environmental influence.

(*d*) That maleness and femaleness are Mendelian characters.

(*e*) That environmental and functional influences, operating through the parent's body, may alter the proportion of effective female-producing and male-producing germ-cells.

These five theories are not in a strict way mutually exclusive.

Even if we conclude that there are, for instance, two kinds of ova in the ovary, one set predestined to develop into males and the other set predestined to develop into females, it does not follow that the relative numbers of these cannot be changed as life goes on, e.g. by the diet of the parent. And even if we conclude that there are two kinds of ova predestined from the start, it does not follow that the predestination need be quite unalterable by the conditions of fertilisation and of development.

Another preliminary caution must be noted. What determines sex in frogs may not hold true for cattle; what determines sex in Rotifers may not apply to birds. Nature is very manifold, and it may be that sex is determined by a variety of factors operative in different cases and at different stages.

(*a*) FIRST THEORY.—*That environmental influences, operating on the sexually undetermined offspring (after fertilisation), may have at least a share in determining the sex.*

In many young organisms it is for a time impossible to distinguish the sexes, and the assumption is often made that there is a prolonged indeterminateness as regards sex. So the first theory that we need discuss is, as stated above, that environmental influences give the bias towards maleness or femaleness.

In support of this theory it has been customary to refer to the interesting experiments on tadpoles made by Professor Emile Yung, of Geneva, who began experimental investigation of the subject at a time when this mode of approach was little thought of.

Let us recall some of Yung's evidence. Tadpoles are said to linger for some time in a state of sex-indifference or potential hermaphroditism. In normal conditions there are about 57 females to 43 males in the hundred. But tadpoles fed with beef, fish, and frog-flesh yielded respectively 78, 81, and 92 females in a hundred. This was, of course, a very interesting result, but it has been pointed out that Yung did not pay sufficient attention to differential mortality, that he had not sufficiently large numbers, and that although some tadpoles are potentially hermaphrodite (with testes around the ovaries), there are others which are quite distinctly male or female even in young stages.

When caterpillars are underfed, there is an unusually large proportion of males (Landois, Treat, Gentry, and others). But as it was shown long ago that the sex of the caterpillar or of the future adult is determined before the larva leaves the egg, starving experiments are irrelevant. They only show that there may be great differences in the rate of juvenile mortality in the two sexes.

Nor is there agreement among the results of experiment. Kellogg and Bell found that the sex of the silkworm is not appreciably affected by the nutrition of the parents or even of the grandparents

as well. Cuénot found that the proportion of the sexes in blowflies, where its visible determination is later than in Lepidoptera, was not affected by what the larvæ ate, or by what their parents ate.

What then is our conclusion in regard to the first theory? Perhaps there is no quite convincing evidence to show that environmental influences operating on a developing organism may decide what its sex is to be. Yet we should be slow to assert that this is impossible. Consider, for instance, Nussbaum's elaborate experiments on *Hydra grisea*, which he subjected to varying nutritive conditions. In this species there are both hermaphrodite and diœcious forms. Nussbaum found that the optimum nutritive conditions resulted in a predominance of female polyps, and that groups wholly male could be produced by relative starving.

According to Baltzer, but *pace* Goldschmidt, the free-swimming larvæ of the Bonellia worm that settle down on the proboscis of old females develop into pigmy males; those that sink into the substratum develop into large females.

There are analogous experiments in regard to some plants. Thus Prantl found that spores of the Royal Fern (Osmunda) and of *Ceratopteris thalictroides*, sown in soil without nitrogenous supplies, developed into male prothalli, that female organs were formed when ammonium nitrate was supplied, and that wholly male prothalli might become wholly female prothalli. In cases like fern-prothalli and Hydra, which may be normally hermaphrodite, what actually occurred in the experiments was probably the inhibition or suppression of one set of sexual organs in favour of another. Nevertheless, the experiments suggest that the first theory (*a*) is not to be dismissed too hurriedly.

Moreover, when we recall how a little nutritive attention makes a worker-grub a queen-bee, or how Aphides produce females parthenogenetically through months (or even years) of high feeding and pleasant temperature, and how the advent of autumn, with its cold and its scarcity of food, is followed by a birth of males, and so on, we may not be able to share the dogmatism of some who assert that the theory of the environmental determination of sex is preposterous. We shall afterwards consider the question of the influence of the environment on the parents.

(*b*) **SECOND THEORY.**—*That the sex is undetermined until the germ-cells unite in fertilisation, when it is decided by their relative condition, or by a balancing of the tendencies they bear, neither sperm nor ovum being necessarily decisive.*

It has been a favourite theory, especially in regard to man and mammals, that the sex of the offspring depends upon the relative condition of the germ-cells at fertilisation, the differences in condition depending on the relative age of the parents and on

other such circumstances. Let us consider various forms of this second theory.

Hofacker (1821) and Sadler (1830) independently published statistics in support of the theory that when the male parent is the older, there are more males among the offspring, and that when the female parent is the older, there are more females. In short, the sex of the offspring depends on the relative ages of the parents. Statistical evidence has been found both supporting and contradicting this theory. Schultze's experiments on mice tell strongly against it.

It seems fair to notice, that *if* the germ-cells remain for some time undetermined in regard to the sex which they will express—if, in other words, they retain for some time the potentiality of either—there is no *a priori* reason against the hypothesis that the absolute and relative ages of the parents may have influence.

Or again, even *if* there are two kinds of egg-cells and two kinds of sperm-cells, which are from the first determined towards developing into females or towards developing into males, the age of the parent may favour the production of one kind rather than of the other, or may favour the survival of one kind rather than of the other.

There seems some evidence in mankind of a correlation between the age of the mother and the sex of the child. The younger mothers tend to have more female children; the older mothers tend to have more male children. On this the self-regulating numerical balance of sex in a nation is said to depend. When females are scarce—for instance, in a colony—they mate early, and supply the demand for girls. When men are scarce—for instance, after war—there are more late marriages, and therefore more boys.

By many authors, e.g. Girou, and at various dates, the theory has been propounded that the sex of the offspring tends to be that of the "more vigorous" parent. This is a favourite opinion among breeders and the fathers of many boys, but it lacks substantiation, and the concept of comparative vigour is too vague to be useful. So far as parental vigour may depend on strained reproduction, or on deterioration supposed to result from close inbreeding, Schultze's experiments on mice do not in the least confirm the view that it has any effect on the proportions of the sexes.

Starkweather was responsible for the theory that the sex of the offspring tends to be the opposite of that of the "superior" parent; but "superiority" and "comparative vigour" are far too vague to be scientifically discussible. We have not been able to discover data warranting the conclusion that a prepotent sire gives his offspring a bias either towards his own sex or towards the opposite.

According to Van Lint, the offspring has the sex of the parent whose sex-cells are the weaker at the time of fertilisation. The sure

and certain sign of a man being "sexually more vigorous" than his wife is their having a daughter. "Le sexe de l'enfant tranchera la question."

It has been repeatedly suggested that a determining factor may be found in the relative maturity or freshness of the sex-cells which unite in fertilisation. Thury and other breeders have maintained that an ovum fertilised soon after ovulation is likely to produce a female. That is to say, the fresher ovum, not exhausted in any way, e.g. by continuing to live without feeding, will tend to produce a female. An older egg tends to produce a male. The bias of the ovum may be corroborated or contradicted by the condition of the fertilising spermatozoon.

As the outcome of prolonged experiments, Prof. Richard Hertwig found that either over-ripeness or under-ripeness of the eggs (due to artificially delaying or hastening fertilisation) led to a large excess of males. Elaborate experiments by Sergius Kuschakewitsch have corroborated Hertwig's results up to the hilt. The proportion of males is largely dependent on the degree of over-ripeness in the ova, and cultures of *males only*—with only 4–6 per cent. of deaths—were obtained.

In connection with fertilisation we may notice the theory of Prof. H. E. Ziegler. He assumes that the chromosomes derived from a grandmother tend to produce a female, and those derived from a grandfather tend to produce a male. He points out that the parental chromosomes include contributions from the grandfather and the grandmother, and since the relative numbers of these depend on the chances of the reduction division in maturation, it will be a "toss-up" whether grandfatherly or grandmotherly chromosomes predominate. If the former, the child will be a boy; if the latter, a girl.

Suppose the potential offspring has 24 chromosomes from the father and 24 from the mother, as in the human species: If the former include 16 grandmother chromosomes and the latter 14 grandmother chromosomes, the child will be a girl, for 30 of the 48 chromosomes are derived from the grandmothers' side.

Probably, however, this speculation is quite inadmissible. We must rid our minds of the view that there is in ordinary cases any necessary *intrinsic* bias in the egg to produce a female, any necessary *intrinsic* bias in the spermatozoon to incite the development of a male.

Our conclusion in regard to the second theory must be: that there is little warrant for attaching much importance to the relative condition of the germ-cells at the time of amphimixis. The experiments of such a careful worker as Richard Hertwig incline us to keep the question open, but O. Schultze's results seem to close it in one case at least. He experimented with enormous numbers of

mice, and found that the proportions of the sexes in mice were unaffected by the age of the parents, by apparent vigour, by consanguineous union, by frequency of births, or by any kind of nutritive change.

(c) THIRD THEORY.—*That the sex is fixed at a very early stage by the constitution of the germ-cells as such, there being female-producing and male-producing germ-cells, predetermined from the beginning and arising independently of environmental influence.*

On this view there are two kinds of germ-cells, constitutionally predetermined to be female-producers or male-producers. This implies that the sex is determined before fertilisation, thus excluding the *second* theory. It also implies that the influence of the environment is negligible after the germ-cells have been established, and *a fortiori* after development has begun, thus excluding the *first* theory.

TWO KINDS OF OVA.—What evidence is there of two kinds of ova—one kind constitutionally predestined to develop into males, the other kind constitutionally predestined to develop into females?

Some animals normally produce two *sizes* of ova. Thus in Phylloxera among Insects, and *Hydatina senta* among Rotifers, there are large eggs which develop into females, and small ones which develop into males. As both develop without fertilisation, the problem is not complicated by the influence of the sperm.

In *Dinophilus apatris*, according to Von Malsen, and in a mite, Pediculopsis, according to Reuter, where fertilisation occurs as usual, there are large ova which develop into females and small ova which develop into males. In Dinophilus, the ovum which becomes a male is only about one-tenth of the size of that which becomes a female, and the male himself is a degenerate pigmy! We must not hastily assume that it is the size that determines the sex, since it may be that the constitutional predisposition to one sex or the other determines the size.

In some of the higher Pteridophytes there are two kinds of spores, micro- and macro-spores, which produce respectively male and female prothalli. A similar predestination, not marked by visible differences, has been proved by Blakeslee in both zygotes and spores of various species of Fungi, and it has also been demonstrated in liverworts and mosses. In the studies of the Marchals on diœcious mosses, isolation cultures prove that the spores, though similar in appearance, are individually predestined, indeed fixedly predetermined, to develop into male or female gametophytes.

The view that there are two kinds of ova, determined *ab initio* as male-producers and female-producers, had a vigorous supporter in Beard, who found evidence in the skate. He maintained that the

sex is determined when the primitive germ-cells divide into oocytes. In his 1902 paper on *The Determination of Sex in Animal Development,* Beard said: "Any interference with, or alteration of, the determination of sex is absolutely beyond human power." To this, an experimenter like Russo would answer that he *has succeeded* in effectively interfering with the determination of sex. For although it may not be possible to alter the bias of an egg which has become fixed to develop into a male or into a female, it may be possible by altered nutrition to change the numerical *proportions* of these two kinds of eggs produced in the maternal ovary, and it may be possible in other ways to change the normal proportions of survival.

Of great interest in connection with this third theory are the facts of Polyembryony—the production of multiple embryos from one ovum. Like "identical twins" the "polyembryonic" offspring

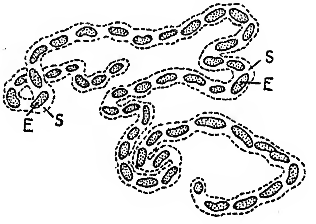


FIG. 77.

Polyembryony of a Hymenopterous Insect (*Encyrtus fuscicollis*). After Marchal. From one ovum there are developed numerous embryos (E), enveloped in a ribbon of mucus (S).

are always of the same sex. In one of the armadillos (*Praopus* or *Tatusia hybrida*) von Jhering found on two occasions eight embryos within one chorion—presumably, therefore, from one ovum—and all were males. In some of the parasitic Hymenopterous insects, e.g. Encyrtus, investigated by Marchal and Bugnion, Litomastix and Ageniaspis, investigated by Silvestri, one segmented ovum forms a group of embryos, all of the same sex—female if the egg be fertilised, male if it be not fertilised. These facts strongly confirm the view that the sex of the offspring is already determined in the egg.

The theory has been more than once suggested that the ova from one ovary develop into females and those from the other ovary into males. Thus Dr. Rumley Dawson (*The Causation of Sex*, London, 1909) has maintained for man, that the ova produced by the right ovary develop into males, and that those produced by the left ovary develop into females. This view has been tested experimentally in the rat by Doncaster and Marshall, who found that each rat,

with one ovary completely removed, produced young of both sexes. The theory has also been disproved in Amphibians by H. D. King. That it cannot apply to birds is obvious, since they have only one ovary.

TWO KINDS OF SPERMATOZOA.—In about thirty different kinds of animals there are two shapes of spermatozoa which differ in certain details. It has been suggested that each kind is predestined towards the development of one sex, but there is no definite evidence that the dimorphism has this significance.

The theory that in Vertebrates one testis yields male-producing spermatozoa and the other female-producing spermatozoa, has been disproved in rats by Copeman. Moreover, as Doncaster and Marshall point out, it is known to stock-breeders that bulls from which one testicle has been removed give calves of both sexes.

THE ACCESSORY CHROMOSOME.—Of great interest are the facts that have come to light regarding what is called the accessory

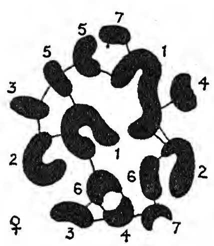


FIG. 78.

The Chromosomes of a Single Nucleus, showing considerable variety in shape and size. After Belar.

chromosome. In a number of Insects, Myriopods and Arachnids, the females have more chromosomes in their cells than the males have. In the simplest cases (Anasa, Protenor) the female has one more chromosome than the male, and the egg has one more likewise. Now half the spermatozoa differ from their neighbours in having the same number of chromosomes as the egg, while the others have one fewer. This extra chromosome which half have, and half have not, is called the X-element or accessory chromosome. There are facts which go to show that fertilisation of the eggs by one class of spermatozoa results in males, by the other in females. When two equal numbers come together the result is a female.

A fine corroboration of the importance of the chromosomes has been recently afforded by the work of T. H. Morgan on Phylloxera and of von Baehr on *Aphis saliceti*. In these forms half of the spermatocytes degenerate (as Meves pointed out in the bee), namely those without the accessory chromosome; therefore all the sperma

tozoa are female-producers, and every one knows that all the fertilised ova produce females. An interesting correlated fact is that in Phylloxera and Aphides the males have in their bodies one chromosome fewer than the females have. "The male-producing egg", Wilson notes, "must therefore eliminate one chromosome, and this, we cannot doubt, is the X-element."

Investigations by Guyer and others point to the conclusion that in various Vertebrates, e.g. fowl, guinea-pig, rat, and man, the male has one chromosome less than the female. Thus man has 47 and woman 48.

The theory that the presence of one X-element in a fertilised ovum means male offspring, and that the presence of two means female offspring is morphological and leaves our physiological sense unsatisfied. Is the difference significant in itself, or as an index of differences in metabolism? If the eggs with more chromatin than their neighbours develop into females and if chromatin be an index of a relatively preponderant anabolic capacity, cannot the theory be brought into line with the thesis of *The Evolution of Sex*, that the female is the outcome and expression of relatively preponderant anabolism, and the male of relatively preponderant katabolism?

Baltzer observed that about half of the eggs of the sea-urchin are distinguished from the others by having one of the eighteen chromosomes represented by a short "hook-chromosome" instead of a normal "rod-chromosome", and there is indirect evidence that those ova with the short "hook-chromosome" develop into males. In discussing this result and comparing it with the state of affairs in the various insects already referred to, Boveri points out that in both sets of cases the fertilised ovum from which a female develops has *more chromatin* than that from which a male develops, and that the amount of chromatin has a regulative influence on the amount of cytoplasm. He suggests that *in some cases* nurtural influences operate variably or unequally on sexually indifferent germ-cells, giving them a bias to the one sex or the other, and that *in other cases* the decision is due to an internal factor such as the presence of stronger "assimilation-chromosomes" in some of the ova. This is in line with the thesis in our *Evolution of Sex* (1889).

On the other hand, it may be that the additional chromatin material is of *qualitative* importance. Thus Prof. E. B. Wilson suggests, quite provisionally, that the X-element contains factors (enzymes or hormones?) that are necessary for the production of both the male and the female characters; that these are so adjusted that in the presence of a single X-element the maleness character dominates, or is set free; and that the association of two such elements leads to a reaction which activates the femaleness character.

(*d*) **FOURTH THEORY.**—*That maleness and femaleness are Mendelian characters.*

A Mendelian interpretation of sex, first suggested by Strasburger, has been developed by Castle, Correns, Bateson, and others. As Wilson points out, the interpretation has taken "three forms, which exhaust the *a priori* possibilities. These are, first, that both sexes are sex-hybrids, or heterozygotes (Castle); second, that the male alone is a heterozygote, the female being a homozygote recessive (Correns); third, that the female is the heterozygote, the male being a homozygote recessive" (Bateson).

Let us state *the third form* of the Mendelian interpretation, which is supported by a number of striking facts, especially in regard to the common currant-moth (*Abraxas grossulariata*) and the canary.

Assuming that there are sex-determinants, "factors" or "genes" of maleness and femaleness, the experimenters suggest: (1) that these behave as Mendelian units, femaleness being always dominant over maleness; (2) that female individuals are heterozygous as regards sex (having maleness recessive) and that they give rise to equal contingents of male-producing and female-producing ova; (3) that male individuals are homozygous as regards sex, being without the femaleness factor, and give rise only to male-producing spermatozoa; (4) that when a male-producing spermatozoon fertilises a male-producing ovum the result is, of course, a male, and that when a male-producing spermatozoon fertilises a female-producing ovum the result is a female, femaleness being by hypothesis dominant over maleness.

Doncaster refers to the confirmation which the Mendelian theory of sex receives from the results of castration. In Vertebrates the castration of the young male may prevent the expression of masculine features, but it does not indnce the expression of feminine characters. This may mean that the male is homozygous, that is to say, purely masculine without any feminine characters latent. We would, however, point out that in many cases there is a lack of positiveness in the feminine characters; while the masculine characters are positive and distinctive. In other words, there might be a good deal of latent femininity in the castrated male, without there being much to show for it. It would be extremely interesting to experiment with some case like the Red-necked Phalarope, where the female bird is the more masculine of the two.

The fact that the proportions of the sexes are sometimes very variable, as Heape points out in regard to canaries, does not of itself tell against the view that the ova are determined at an early stage to be male-producers or female-producers. There may be a process of discriminate selection during the maturing of the ova, and we know that in higher Vertebrates the possible ova do not all come to maturity.

(*e*) FIFTH THEORY.—*That environmental and functional influences, operating through the parent's body, may alter the proportion of effective female-producing and male-producing germ-cells.*

This, like the first theory, admits the importance of nurture (in the wide sense), but supposes it to be influential *at an early stage* in determining the proportion of effective female-producing and male-producing germ-cells. Supposing that the original germ-cells are of two kinds, male-producing and female-producing, we can conceive that nurtural conditions may sometimes influence the relative rate of increase or the percentage of survival in the two groups. Or supposing that the immature germ-cells are constitutionally indifferent, we can conceive that nurtural conditions, such as a change in the nutrition of the parent, may sometimes decide their destiny.

It seems fairly clear that there are many cases to which this theory of nurtural determination will not apply at all, e.g. when numerous young are born at once and show an approximately equal distribution of the sexes.

On the other hand, there are cases where a mother produces a long succession of offspring all of one sex, or produces one son and a long succession of daughters, and so on. Such cases suggest that the constitution of the parent may be of some importance, and we know that the constitution is modifiable by nutrition and the other factors in nurture. When we pass from general considerations such as the above and appeal to the facts, we find an interesting conflict of evidence.

From human statistics some have tried to prove that abundant food favours the production of female offspring, and vice versa; but others have concluded, also from statistics, that the parental nutrition is of no moment, unless in bringing about a differential death-rate. The fact that 30 per cent. of human twins are of different sexes seems enough to show that the dieting of the parent is not of great importance.

Careful experiments have been made, e.g. by Cuénot and Schultze, on the possible influence of the nutrition of the mammalian parent (e.g. mouse) on the sex of the offspring; but the results are all against the reality of this supposed influence, in which, however, some breeders strongly believe. Schultze extended his experiments over three generations, but the high feeding of grandparents as well as parents did not seem to have any influence on the proportion of the sexes among the offspring.

Against these results, however, we have to balance the very important work of Heape, who has brought forward evidence for mammals and birds that peculiarities in nutrition and in other environmental influences may exert *a selective influence* on the germ-cells, affecting the proportion of male-producing and female-producing gametes.

Of great interest and importance are Russo's experiments in treating rabbits with lecithin. They support the view that the germ-cells may be predisposed to one sex or the other by the nutritive condition of the parent, and the view that the difference between the sexes is primarily a question of the rhythm of metabolism. Russo attaches much less importance to the chromosomes and much more importance to the nature of the metabolism than do most biologists of to-day. He believes that the sex of the offspring depends on the special metabolism of the germ-cells; and he thinks he has succeeded in artificially altering the metabolism of the ovarian ova, and thus altering the normal proportions of the sexes. In the normal ovary there are well-nourished and ill-nourished ova, and the proportion of the former can be increased by lecithin treatment.

Female rabbits treated by injections of Mercks' lecithin developed large ovaries, large Graafian follicles, ova rich in nutritive material, and eventually an unusual number of female offspring. The sperm may, as it were, corroborate the bias of the ovum, for the percentage of female offspring is higher when both parents are fed with lecithin. It is not possible to follow the ova and prove that a relatively anabolic ovum always becomes a female, and never a male, but the argument from altered proportions seems sound. While the lecithin treatment is followed by an increase in the number of ova of "an anabolic type, rich in lecithin globules", it may happen that the *first* litter after the beginning of the treatment shows a marked preponderance of males. This Russo regards as due to the fact that the injections stimulate the general metabolism and inhibit the degeneration of the ova of the katabolic type, capable of producing males. The increase in the number of females occurs subsequently.

Several investigations support the view that changes in nutrition and other environmental conditions may affect the mother so as to alter the ordinary proportions of the sexes. Thus Issakowitsch, working with the parthenogenetic females of the Daphnid Simocephalus, and von Malsen, working with *Dinophilus apatris*, in which the ova are fertilised, found that differences of temperature affected the proportion of the sexes, apparently by affecting the nutrition of the mothers. Both sets of experiments are the more satisfactory that they seem to be free from any fallacy due to differential death-rate in the young of the two sexes.

Against the theory of environmental influence are Strasburger's numerous experiments on diœcious Phanerogams, such as *Mercurialis perennis*, spinach and hemp. He found that changes in illumination, soil, crowding, and so on, had no effect in altering the proportions of male and female offspring.

As regards the fifth theory, then, we find: (I) that in certain cases there is some evidence that the nurture of the parents may influence

the proportions of the male-producing and female-producing germ-cells, affecting either the number formed or the number that survive, and (2) that in other cases there is no hint of any such influence, the facts pointing rather to the view that the sex of the future offspring is not only predestined but predetermined at a very early stage in the germ-cells. Looking back over the array of facts of which we have given samples, we would say, with Dr. F. H. A. Marshall, that they point to the conclusion that "the sex of the future organism is determined in different cases by different factors and at different stages of development—either in the unfertilised gamete, or at the moment of fertilisation, or in the early embryo".

A PHYSIOLOGICAL WAY OF LOOKING AT THE FACTS.—To the physiological view of sex, first expounded in *The Evolution of Sex* in 1889, a brief reference must now be made, for we find ourselves unable to get away from the conviction that there is no sex-determinant or factor at all, in the morphological or in the Mendelian sense, but that what settles the sex is a metabolism-rhythm, a relation of nucleoplasm and cytoplasm, a relation between anabolism and katabolism.

All through the series of organisms—and of animals in particular—from the active Infusorians and the passive Sporozoa, to feverish Birds and sluggish Reptiles, we read alternatives or antitheses between liberal expenditure of energy and a more conservative habit of storing. This primarily depends on the ratio between disruptive (katabolic) processes and constructive (anabolic) processes, and we regard the sexes as expressions of the same contrast within a given species.

According to this view, the deep constitutional difference between the male and the female organism, which makes of the one a sperm-producer and of the other an egg-producer, is due to an initial difference in the balance of chemical changes. The female seems to be relatively the more constructive, whence her greater capacity for sacrifices in maternity; the male relatively the more disruptive, whence his usually more vivid life, his explosive energies in action. In short, the sexes express a fundamental difference in the rhythm of metabolism.

This initial difference not only leads to the primary functional distinction between male and female, but it also determines, either from the start, or after maleness and femaleness have been in part established, what particular expression will be given to a whole series of secondary characters—both structural and functional—whether a masculine or a feminine expression.

Many sets of facts lead one to conclude that each sex-cell has a complete equipment of masculine and feminine characters, and it may be that the liberating stimulus which calls the one set or the

other into expression or development, is afforded by the metabolism conditions that have been set up in the cytoplasmic field of operations, which lead also to the establishment of spermary or of ovary, as the case may be.

It may also be noted that in thinking of the general question of the Determination of Sex, we are probably on safer ground when we pass from the higher animals with their highly specialised dimorphism—familiar in peacock and peahen, ruff and reeve, lion

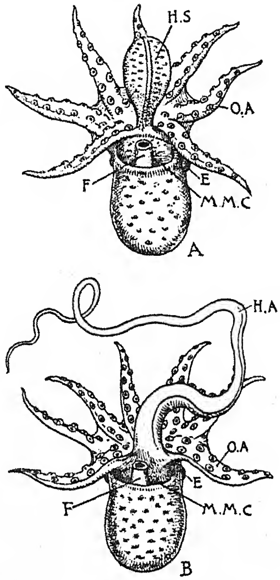


FIG. 79.

Male of Paper-nautilus (Argonauta). After Jatta. A shows the ordinary arms (OA) and a much modified arm laden with spermatophores within a "hectocotylus sheath" (HS). E, eye; MMC, mantle cavity; F, funnel. In the lower figure (B) the transformed arm (HA) has been much elongated beyond the sheath.

and lioness, man and woman—and get down to the lower reaches where, as in starfishes and sea-urchins, it is often impossible to distinguish the two sexes without a microscopic examination of the reproductive organs.

It is profitable to press the problem further back to its simplest expressions, such as we see, for instance, in Volvox, that beautiful sphere of flagellate cells which so well illustrates a body in the making. From the ball of cells reproductive units are sometimes set apart, which divide to form other colonies without more ado. But in other conditions, when nutrition is checked, a less direct mode of

reproduction occurs. Some of the cells in the ball become large, well-fed elements—the ova; others, less anabolic, fading from green to yellow, divide and redivide into many minute units—spermatozoa. The large cells of one colony are fertilised by the small cells from another. Here we see the formation of dimorphic reproductive cells in different parts of the same organism. But we may also find Volvox balls in which only ova are produced, and others in which only sperms are produced. The former are more vegetative and nutritive than the latter; we call them female and male organisms respectively; we are at the foundation of the differences between the two sexes.

What we are suggesting is a physiological way of looking at the problem, and the idea that the sex-contrast expresses a physiological alternative. This is suggested in various ways. For instance, there is the sometimes striking evidence that sex is "a quality that pervades all the cells of the organism". Prof. Wilson notes the extraordinary fact—surely of profound importance—that: "In the Mosses the Marchals demonstrate that all the products of a single spore are likewise immutably determined, since new plants formed by regeneration from fragments of the protonema, or from any part of the gametophyte, are always of the same sex."

It is interesting also to consider cases where the sex changes in the course of life! A case carefully described by Prof. F. Braem is very suggestive. He experimented with a simple Annelid worm, *Ophryotrocha puerilis*. Taking a female which had ripe eggs and showed no trace of hermaphroditism, he divided it into two. The head portion, with thirteen segments, was isolated. In three weeks it had regenerated seven segments with parapodia. It was then killed and found to be male. The ova had mostly disappeared from the reproductive organs, leaving only a residue, and a functional testicular portion had developed, which was producing spermatozoa. Braem suggests that in consequence of the amputation the very young, indifferent germ-cells had developed into male cells, which require less subsistence than ova. What is certain is that the reproductive organs had changed from producing eggs to producing sperms, and such cases appear to us to favour the view that the sex-difference is fundamentally physiological.

Conclusion.—In conclusion, our view is that the difference between an ovum-producer and a sperm-producer is fundamentally a difference in the balance of chemical changes, i.e. in the ratio of anabolic and katabolic processes, which may, of course, have its structural expression in the relation of nucleoplasm and cytoplasm. Nor do we leave this difference in metabolism-rhythm as a mere vague phrase, for we see its analogue in the contrast between the ovum and the spermatozoon (though it is quite unwarrantable to think of these as being in themselves respectively female and male

cells), between the macrogamete and the microgamete, between the encysted and the flagellate cell, between the plant and the animal, and in many a familiar contrast all through the series of Organisata. We adhere, in short, to the thesis of *The Evolution of Sex* that the sex-difference is but one expression of a fundamental alternative in variation, to be seen throughout the world of life.

Can We Control Sex?—Not many years ago it would have seemed very "academic" to discuss the validity of the Manoilov test for sex, or to speak about chromosomes in their relation to the sex of calves and chickens on the farm. But we are more broad-minded nowadays, especially since it has been proved up to the hilt in instance after instance that very theoretical investigations are often of the highest practical importance. As Bacon said, they are fruit-bearing as well as light-giving.

Now from several sides the citadel of sex is being stormed, and the theoretical questions to which we have been referring are essential parts of the attack. Suppose it be true that the sex of the offspring depends primarily on the rate and rhythm of the metabolism (or essential biochemical routine) in the egg-cells and sperm-cells, then it may be possible to sway the metabolism to one side or the other by altering the influences that play upon the germ-cells. It may be possible to speed up or slow down the oxidations of the egg or of the developing embryo. In some lower animals this has already been done in various ways, and it may now be said that sex is theoretically transformable or controllable. And apart from the possibility of getting twelve cockerels to the dozen, and all that sort of thing, a deeper physiological understanding of sex may lead to methods of correcting sex-deficiencies or sex-exaggerations in human beings. We quote a couple of sentences from one of Prof. Riddle's recent papers: "Very diverse and special methods have been used in controlling sex in several animals, but these are at present largely or wholly inapplicable to the human and other mammals. Yet if the ultimate effects of these several methods are reducible to changes in what is known as metabolic rate, we can later hope to employ in man and mammals other and new agencies which can act directly and specifically on metabolic rate in the egg and embryo."

REVERSAL OF SEX.—There are some quite normal animals that change their sex in the course of their lifetime. Thus the curious primitive vertebrate called the hagfish (*Myxine glutinosa*), which is far below the level of true fishes, which lives in deep water in the North Sea and elsewhere, and sometimes bores into moribund or dead fishes that have been caught on the fisherman's "deep lines", is said to be first male and then female. This at least is the outcome

of two sets of investigations by Mr. J. T. Cunningham and by Nansen (who was long a productive zoologist).

Specimens below a certain size are said to be all males; those above a certain size, about a foot, are said to be all females. This means that as the hagfish grows to maturity, its unpaired reproductive organ changes from being a sperm-producer to being an egg-producer.

There is a little starfish (*Asterina gibbosa*), found in European waters, which is first male and then female, with an interesting intermediate phase when it is both, or, in other words, a transient hermaphrodite. This is a very interesting case which deserves further study. Even by itself it is enough to show that sex is not necessarily a rigidly fixed constitutional state, but rather a physiological phase, to some extent plastic and even capable of swinging to the other extreme.

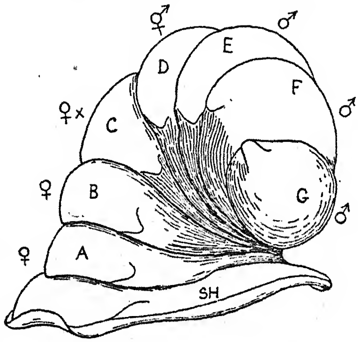


FIG. 80.

Group of Slipper Limpets (*Crepidula fornicata*), one on the top of another. After Orton. SH, the basal shell; A, B, C are female; D is a hermaphrodite; E, F, G are males.

Very extraordinary is the story of a limpet-like animal called Crepidula which has been introduced into English waters from the United States, and has been carefully studied at Plymouth by Dr. J. H. Orton, as well as by Conklin and by Gould, two American zoologists. The actively locomotor young forms are males, but after they settle down on oyster-shells, or the like, they become hermaphrodites or neutrals. Later on they become females. In some species they have the habit of fixing themselves on others of the same kind, so that there may be seven individuals, one on the top of another, the lowest and oldest being fixed to a shell. It looks as if they had borrowed an idea from the American skyscrapers.

Of the seven, to take one of Dr. Orton's cases, the youngest three may be males, the fourth a hermaphrodite, and the oldest three

females. But these females were once males! For the remarkable fact has been discovered by Gould that in the species called *Crepidula plana* the newly fixed forms are mostly hermaphrodites, which change quickly into females; but if these young neutrals are brought into the proximity of large individuals they become males! Or if the young fixed individual was a male, it will remain for a considerable time a male, instead of hurrying through that phase, provided a big-sized neighbour is present.

The big-sized individual may be a male or female; the nature of its influence, that slows in its neighbour the passage into the female

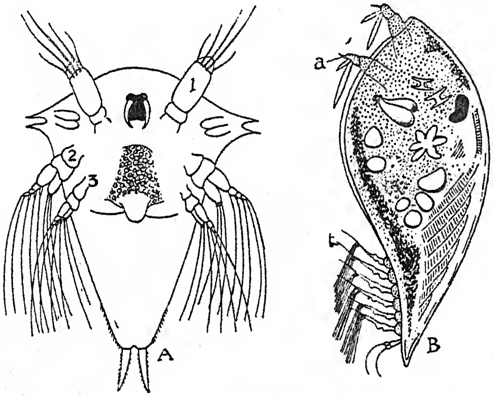


FIG. 81.

Two Stages in the Life-history of Sacculina. After Delage. A, the nauplius, with three pairs of appendage (1, 2, 3). B, the cypris or pupa stage, effecting attachment to a crab; a, antennæ; L, swimming appendages. The eye is shown dark in each figure.

state, remains quite obscure. But this case of the Slipper Limpet is enough to show that sex is more plastic than is usually believed.

We have already referred to the Mediterranean worm, Bonellia, of a beautiful green colour. The female is about the size and shape of a prune, unwrinkled; but a long, narrow contractile proboscis protrudes for ten inches or so from the mouth and ends in two ciliated lobes. But the male is a very different creature, and no ordinary observer will discover him at all. He is degenerate and practically microscopic; he lives inside his giant mate! For our present purpose the interesting point is this: the microscopic larvæ of Bonellia are free-swimming for awhile, and after that they settle down. If one settles down in the mud on the floor of the sea, it develops into a female. But if one adheres to the proboscis of a female, it develops into a male!

Of great interest in this connection are the studies made by

Geoffrey Smith and others on crabs that fall victims to parasitic crustaceans distantly related to barnacles. One of the best known is called Sacculina, which is occasionally found on the sea-shore, protruding like a kidney-bean on the under side of a crab. The young Sacculina, after a period of free-swimming, first as a nauplius, then as a cyprid lava, fixes itself to a crab, works its way into the interior, and grows greatly at the expense of the tissues of its host.

It eventually protrudes on the outside, beneath the shelter of the tail. Let us suppose, for simplicity's sake, that the parasitised crab is a growing male; its constitution soon begins to be profoundly altered. Its tail broadens, approaching that of a female; some additional appendages develop on the tail, which are characteristic of the female, though smaller in size; the composition of the blood seems

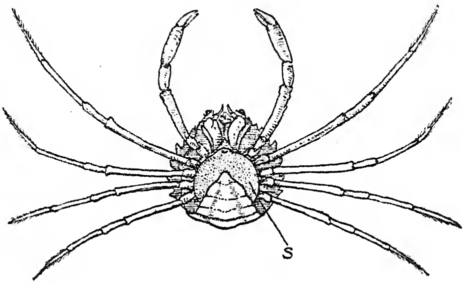


FIG. 82.

A Crab, Inachus, Parasitised by a Rhizocephalan Crustacean, Sacculina (S), which brings about castration. After Geoffrey Smith.

to be altered; and, most remarkable of all, the male reproductive organ begins to show some eggs. Here we see sex partly changed by a parasite!

But, it may be asked, are these changes of sex confined to the lower animals? The answer is that several cases of sex-reversal in vertebrates have been demonstrated in the last few years. Champy, a French investigator, showed in 1920 that a male newt, which had fertilised the eggs of a female, became, as the result of prolonged fasting, indistinguishable from a typical female. Its reproductive organs were found to be full of immature ova. Very carefully studied is Prof. Crew's case of sex-reversal in a hen.

Some time earlier, but not quite so convincingly, Prof. Riddle produced evidence of complete sex-reversal in a ringdove. Both the hen and the male bird suffered from tuberculosis. We have said enough to show that sex is not necessarily fixed, once and for all. It is plastic; it may be reversible!

THEORY OF SEX

As regards the evolution of sex, we still firmly maintain the general theses of the volume so named in 1889, and of its further developments in *Sex* (1914). For in these two books, the origins of sex are traced upwards from the general biochemistry of protoplasmic metabolism; and are based in the appreciable preponderance of anabolic processes in the female sex, and of katabolic in the male; which we thence traced through many plant and animal forms, not simply from the large and well-grown ovum and its small and active fertilising element, but also correspondingly in that cell-cycle between passive and active forms which appears to us fundamental to the origin and classification of the Protozoa. In higher and higher forms this sex-process and contrast is increasingly significant; witness, for instance, that rhythmic alternation of generations, in which the asexual generation is so commonly the more vegetative, up to its extreme culmination in the flowering plant. Or returning to the ordinary succession of generations, we sought, in that elemental conception of sex, the origins of the often striking contrast of the sexes in so many animals which the hypothesis of sexual selection was so long the only endeavour to explain. For the more active katabolism of the male seems the natural source to originate such variations, though, of course, the associated female selection is by no means thereby excluded. In passing, however, it may be noted that while Darwin's essentially psychological hypothesis of female selection is congruent with his later and illustrious development as one of the main founders of evolutionary and comparative psychology, it is in very thorough contrast with his earlier-formed view of variations in general, as in no wise psychic, but simply organic—and "spontaneous and indefinite" (at least in the sense of unexplained): whereas a psychologic factor in variation is the essential distinctiveness of Lamarck's doctrine, and not that mere environmental modification, nor assumed use-inheritance, which are so commonly taken as the essential feature.

Returning to sex itself, and to our past volumes, with their theses still maintained—and now frequently confirmed, from biochemistry upwards—the fact remains that after more than a whole generation these are still far short of general acceptance. This we take to be primarily explained by the prevalent morphological interest in microscopically working out the particulars of cell-division, and of nuclear structure and behaviour, amazingly intricate and interesting throughout histology generally, and particularly so in the reproductive cells and their observable processes, and here with keen search for light upon the difficult problems of heredity. So far of course well: yet all these structural discoveries do not and cannot exclude

the needs of physiological explanations also; and thus and from its basal conception of metabolism onwards. Still, we have also frankly to confess much the same inability precisely to apply this to the forms and behaviour of the nuclear elements—the chromosomes for special instance—as their observers as yet do in the converse way. Here, in fact, further research is needed from both sides; and this seems bringing increasing promise of harmony; as seems probable from recent work, such as that of Crew, one of our ablest investigators of genetics and sex.

Yet beyond this we have ventured much further, as to the application of this sex-contrast, with its physiological interpretation—as of more passive, vegetative, and enduring femaleness, with more active and katabolic, so less enduring maleness—into the never-

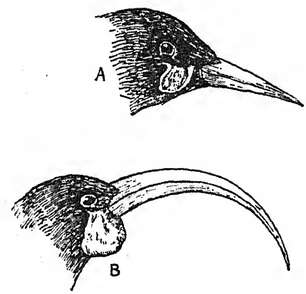


FIG. 83.

Sex-dimorphism as Shown in the Contrasted Beaks of the Male (A) and the Female (B) of the New Zealand Huia (*Heteralocha acutirostris*). The cock chisels away the decayed bark, while the long-beaked hen probes the crevices for insects, thus illustrating division of labour as well as dimorphism.

ending problem of the origins of species, and even genera, orders, etc., and even to the fundamental divergence of plants and animals themselves. That allied species, genera, and groups of many kinds —witness sheep and goats, cattle and buffaloes, or bees and wasps, moths and butterflies, etc., are strikingly feminoid and masculoid in general aspect respectively, and that this contrast prevails even in habits, and so in psychology, so far as we can discern it, is a conception we again submit as worth thinking over, and testing more and more extensively throughout many branches of taxonomy. We do not claim that we can always verify this: but it is surely significant to find it so frequently recurrent, as a steady scrutiny of the collections of any great museum will show. In this connection, too, it is worth recalling that in a good few species the sexes have at first been referred to different genera by taxonomists, witness, for instance, among the amphipod Crustaceans, Praniza and Anceus, now united under the former name. This contrast seems related to

the demonstration by geneticists of the fairly wide existence of sex-gradations, such as we are broadly familiar with in our own species—in which we characterise some men as manly, others as effeminate, and see all gradations between—and also unmistakably among women, as from the most womanly to the most mannish. So now, given the like among many other species—indeed, why not more or less among all?—have we not here a wide possibility, especially through analogous and congruent pairings, of the evolution of the masculoid and feminoid varieties, and thence to species, genera, etc.? In humanity, both similar and contrasted pairings seem each not unfrequently to occur, though we know not with what results; so this matter may be worth more attention from eugenists than it has yet received.

Pass now to what is by far the most prominent line of sex study of recent times, that initiated by Freud. His has been a line of approach altogether beyond our range, since essentially concerned with the excessive sexualism and morbid sex-pathology of our times, and these as hypertrophied in great cities especially. Yet the broad correspondences of these two polarly distinct lines of inquiry are more striking than is their contrast. As naturalistic students of sex, and so of this as the very maturation and culmination of animal and plant individuality and beauty, as from peacock to rose, and thus also towards the like in human life, we have been in company not with the physicians and pathologists, but rather with the artists and poets: so that indeed we may now confess that this theory of sex and its development was for us as nature-students what our friends' paintings and lyrics were for them—and for the like fundamental personal life-history reasons. So in all ways, naturalistic, human, and personal alike, we could not but substantially realise and agree that

> All thoughts, all passions, all delights,
>   Whatever stirs this mortal frame,
> All are but messengers of Love,
>   And bear his sacred flame!

Here, then, is an example of how, long before either naturalistic studies or pathologic discoveries and interpretations, the poets have been voicing Life and Sex in their compenetrance; and all this since who knows how early times—for poets, naturalists, and physicians alike are but Life's children, beginning to understand her. The superiority first of the poets, and now of the physicians, over us mere naturalists is obvious; for the song of the poet springs from his own subconscious depths, and it is the physician's merit to have recognised these; while naturalists have been too simply fascinated by the objective and organic aspect and interest of living beings. But if Freud, with his strong intuition as well as searching

investigation of the subconscious, were also a naturalist, what a super-neo-Lamarckian would he not be!

Again, too, if his dream-world had been more of his own poetry, and less of others' follies and sins, what strange new strains might we not have had! And if his earnestness of life, at once scientific, medical, and Hebraic, had found time to develop and voice his own ethical idealisation of sex to the world, as well as for his relieving the unethical irrealism of others, what moral and even prophetic influence might he not have exerted! Yet towards this he and his school—happily not all docile followers, but with some divergent originality too—have not only been preparing the warning diagnoses and interpretations of salient evils, but actively labouring towards liberating and even redemptive treatment, and even prevention also. Yet for that re-moralisation of sex and youth which is so long overdue—and surely seldom more needed, if our cities, and country too, are to be redeemed from sins and miseries—we need also a more definite turning to higher ideals, and these not only Olympian, and even Parnassian, but even beyond; as the old religions, the antique chivalries, in their way and day, have each striven to show. That the heritage of social life is deeply burdened with evils, and that the heredity of each and all of us is more or less weakened or tainted too, are our modern scientific ways of confirmation and restatement of old doctrines, as of "the Fall", and of that "visitation of the sins of the fathers upon their children", and these with their "original sin" from earliest ancestry—indeed, as we now discern, all latent and potential, and on both the self-maintaining and the species-continuing sides of life. The old ideals and endeavours towards dealing wisely with such evils, by actively guiding their potentialities from evil towards good—which religion has termed "redemption" or "new birth", achieved after due penitence and purgation—are similarly reappearing in modern etho-psychologic terms and methods: as even to the psycho-analyst's renewal of the confessional, with his practical demonstration of its uses, and verification of its sequels. "Prayer" also reappears, as renewed aspiration, confirming purpose and strengthening endeavour towards the better life. And so on: thus in fact William James' brightly predictive interpretation of the coming in of outward hygiene as presage of inner purification of life is coming true. So even are confirmed and renewed other old and high predications and predictions; witness their tradition—vital in all its four senses, bodily, mental, social, and ethical—that the urges of life, however misapplied by egoism or by sensuality, may be "sublimated"—say, rather, transmuted—to high and higher purposes. For here is the very essence of ancient ethical teachings and practices: witness asceticisms and chivalries at their best; as often homely life as well.

Such ethico-social need, urge, and endeavour go deeper and point

higher than do our current social, political, and economic doctrines and endeavours, or our current scientific labours either. All these, indeed, derive more of their energies from sex-sources than they realise; yet all alike need these re-moralised, if they are to realise their best aspirations and their achievements. Yet conversely, too, our vital urge needs support from all that psychology, biology, and social science can discover, and all that etho-policy can realise. And in face of appeals from our cities, at once so inspiring and so piteous —as, for type-instance, that of Jane Addams, that virtual, since true and great, "Abbess of Chicago", in her book of *The Spirit of Youth on the City Streets*—all the interpretations and forecasts that the sciences can offer, all the practical appeals and efforts that wisdom can guide, are alike urgently needed; and these synthetised in thought and mobilised into action. The old ideals thus retain high values; and though these be now more or less isolated, or cloistered —as of Olympus or Parnassus, Eleusis and Delphi, for the scholar; of Zion for Israel; Benares for Hinduism; Sarnath for Buddhism; and Jerusalem, Rome, or Geneva for Christian groupings; or Mecca for Islam, etc.—their pilgrimages, continued from of old to this day, show that these ancient springs are still unexhausted. So, too, mediæval Benedictines and Renaissance Jesuits (though each in their own way coming abreast of science more than its lay votaries generally notice) are above all still drawing inspiration from their mounts of origin, Cassino and Montmartre. Indeed, our romantic poets and composers often also find their Helicon, be this from Garde Joyeuse or Montsalvat.

Yet science must work onwards in its own ways, by turns observant and interpretative: so here we have to ask, first of all, what biology and its associated psychology can offer. As evolutionists, and of sex, we must begin then on the animal level: so best take frankly one of its most simple and familiar types—say, for choice, the common and domestic swine—with whom the prodigal, whether of self- or sex-hunger, comes to be appropriately associated. The sow, then, has her insistent passion of sex allayed, say, indeed, so far sublimated, by her simple and ample maternity: while for active passion, even to combativeness, what more vivid type than the boar? She has affection, he, conspicuously, has courage: so here appear already the two-sexed meaning of the Latin *virtus*; and as clear fundamentals of the respective sex-morals. Yet on higher levels affection normally increases in the male; so towards truer and fuller partnership; whence monogamy, and this with fuller and with more active parenthood: and these we see in Nature, often to varied and admirable perfection, as in so many birds and mammals. Among these, too, a higher progress is discernible. Feminine affection comes to be reinforced by courage; and this not only to defence of young, but also as monogamy evolves, to purity, with loyalty to

mate. Again, in the male, as affection deepens and extends, we have that courageous devotion which in man we call chivalry, yet see the beginnings of in Nature, as even by the barn-door.

Chivalry may be more and more inspired by purity; as to that combination of ascetic idealism and intensity with adventurous, heroic, and even spiritual quest, which inspired the tale-tellers and singers of the Arthurian and mediæval cycles, and again the romantic writers of later days. And correspondingly for the feminine type, which at its higher levels has ever inspired man towards ideals, and to their realisation as well. Here Jeanne d'Arc is the salient type of woman whose heroic idealism has not only inspired action, but even headed it; hence with her brilliant and tragic epic of real life surpassing those of romantic chivalry. And though women and men of such spirit and career no longer bear armour, nor often attain to glorious achievement, some of their like ever reappear, and may more frequently. Thus, in her own way and times, the character and career of St. Teresa present another illustrious example of the union of spiritual insight with constructive leadership; nor has she been without successors; but has now and then a modern analogue still.

An outline so bare as the above obviously admits of fuller development: but it indicates one line of psychobiological approach towards an ethic of the sexes, and with these mutual influences uniting towards their best. But so far there has been no question of the evils with which sex-development is beset; nor yet of those which arise from the converse cause, of individuality repressed for lack of it. Here the conception of life, as essentially bi-systematic—i.e. nutritive and self-maintaining as well as reproductive and species-continuing—affords us a scale on which steps of ascent can be marked, and corresponding descents and deteriorations also. So this may be expressed simply and clearly as a graph starting with N and thence proceeding to R, for nutritive and reproductive systems respectively; the latter with its later development expresses also a fuller maturation of N, a higher individuality N_2. On the next R_2 level, offspring appear, again with heightened individuality, that of parenthood (N_3). On the next level families are associated by ties of kin, R_3, with heightened and broadened personalities once more (N_4). Above and beyond this level we may mark out successive higher spaces for wider and wider relations, those of social groupings from small to greater, and to greatest attainable, with corresponding opportunity and exercise for individualities higher and higher again, and more fully and widely humanised accordingly. So far, then, the ascent of individuality in its organic and social development, and up through successive stages above the initial self-regarding and pre-reproductive level. Yet conversely, below this base-line there appear, and too readily, corresponding levels of descent. For in man the nutritive life may too easily degrade to

gluttony or intemperance, thus lowering individuality; and the normal reproductive life may deteriorate to mere sexual sensuality, with debasement further. So mateship may be degraded; next family neglected; and wider relations lapsed from, and those perverted even to treasons to the highest causes above. In short, then, we have here, in briefest outline, a veritable section through the deepening circles of the Inferno; and these essentially as Dante depicted them. His direct answer to his simple questioners of—"How came you to see hell?"—"In the city around me!"—was thus what we again too often see around us to-day. Yet so, and more happily, does not our ascending ladder recall that of Jacob's youthful vision, of his coming patriarchate; and with its "ascending and descending angels" as the ideals, both immanent and transcendent, of his coming family, with their resulting tribes, rising to nation, and this to its culmination towards the highest.

A kindred orderly line of interpretation of organic and human sexes in their development-phases (with possible deteriorations also) is that outlined upon the Olympian Circle (page 570). Similarly the more general Theory of Life (Chapter xiii) logically develops into a presentment of the Muses as normal to life's evolution; yet also with their possible deterioration, even to perversion and possession by the Furies. All the classic mythologies we can look into have thus in their various ways broadly and vitally anticipated our evolutionary science; and we may thus use and adapt their vivid imagery anew.

Illustrations might here be amplified of how biologic studies disclose anew the old evolutionary ways from life's beginnings with hunger and struggle, to ideals, and towards the highest; and also of how they aid our understanding of the degenerations and perversions of the norms of life.

PARENTAL CARE

It is a conspicuous fact of life that many animals look after their offspring in a very effective way,—often expending much time and energy in securing their welfare. Unless we are willing to leave much of this parental care unintelligible, we must credit many of the higher animals with genuine parental feeling. When the young ones remain for a considerable time with the mother, or with both parents, receiving nurture and protection and a great deal of attention, there seems to be an undeniable evocation of parental emotion. Unless there is some illusion, the parent enjoys having its young one as a companion; it watches it with evident pleasure in its eyes, certainly with great interest, if not with pride; it defends it with courage and in spite of wounds—at the risk of its life, we might say,

if the idea were not too subtle for an animal. Apart from what is sometimes too generously appraised, especially in domestic animals, there are scores of well-observed and carefully described cases where the parent shows courage and persistence in protecting its offspring. The parent is often ill at ease, if not anxious, when the young one is removed; it often shows signs of grief when the young one has been killed. We cannot make sense of what we observe unless we credit animal parents, among birds and mammals, with some degree of parental emotion.

This is not, of course, to assert that the whole parental behaviour is controlled by fine feelings of affection or devotion, for body and mind work together. Often, no doubt, the caresses of the offspring are sensuously pleasant to the parent, and the mother's fondlings are not without a reflex reward. Moreover, there may occasionally be some subtle linkage between "love of children" and "love of mates", especially in cases where the male parent takes on the normally maternal functions of nurture, as in the Sea-horse (Hippocampus) and the Nurse-frog (Alytes).

It is also highly probable that in some instances the parental solicitude is connected with a dawning sense of possession or property. The scarabee beetle objects to having its ball of camel's dung stolen by a neighbour; a mother-spider objects to the removal of the silken bag or cocoon in which she carries her eggs or offspring. Between these two cases may we not place the jealous objections which not a few birds offer to the intrusion of a neighbour on the selected "territory" where the courting goes on and where the nest is eventually built?

The analysis of the parental emotion is a difficult problem for the psychological expert; what the naturalist is chiefly concerned with is the reality and the value of the emotion. It forges psychical bonds between parents and offspring—psychical bonds which strengthen physical endeavour and may sustain the offspring-regarding efforts when the simpler and more physiological appeals of the offspring are no longer potent. The pleasurableness of the parental emotion has indirect survival-value because it makes the patience and sacrifice involved in parentage more attainable. The playsomeness of many young mammals is probably a useful rejuvenescent factor, helping to keep the parents young. In some cases the parent mammal plays year after year with successive families. Finally, the parental emotions are probably in many cases indispensable in evoking the individual development of finer feelings of an altruistic kind, which reach their climax in kin-sympathy and social loyalty.

On the other hand, we must avoid the extreme of over-generosity. It is unnecessary to credit a mother fox with the parental pride so familiar in mankind. For in all probability the devoted carnivore-mother is a long way from being able to say to herself: This is my

offspring, my very own. For that is a somewhat subtle idea, reaching beyond the vixen's wideawake determination that no intruder is to be allowed to come between her and her cubs. How exactly she feels no one can tell, but we are here simply concerned with defending the common-sense thesis that the mammal-mother or the bird-mother has real affection for her offspring and delight in their presence. Why the emotions should gradually wane away as the offspring cease to be young is a problem by itself; but allowance must be made for the limitedness of the animal mind, which passes readily from one preoccupation to another. New interests and problems, or older ones revived, crowd out the parental affection; moreover, the youngsters cease to make their childish appeals and may eventually become intolerable rivals. And while we are insisting that the mental aspect—the stream of feeling—is a *vera causa* that counts for much, we are not for a moment denying that its activity may wane away because of profound changes in the body to which the mind is thirled. *Nemo psychologus, nisi physiologus;* and vice versa. Emotions are real, and so are the endocrine glands; perhaps they are the two sides of one shield.

Now let us pass from the highest animals to near the foot of the inclined plane on which the grades of parental care may be arranged. There we find many cases where the eggs develop in contact with the parent, being attached to the skin, as in the brook-leech and the Surinam Toad, to some of the limbs, as in the crayfish and the sea-spider, or in some sort of pocket, as in some quaint fishes, or in some other way. This carrying of the eggs is an advantageous adaptation, with its counterpart in plants, which secures their safety; and it points the way to those cases where the young ones are similarly carried about for a prolonged period. Being accustomed to carrying the eggs may make it easier for some simple animals to acquiesce in carrying the young; and the automatisation of this is illustrated by those male crabs that have been castrated by a Cirriped parasite (Sacculina, etc.), and behave, in their strangely feminised state, to the protruding parasite as if they were females and it a bunch of eggs. In the lower reaches of parental carefulness the physiological aspect is dominant. Moreover, it is not difficult to find reasons why the newly hatched young, on their part, should sometimes adhere to the congenial safe surface afforded by their mother's skin. Their protoplasm in the course of development has become accustomed to it.

In a few female sea-cucumbers or Holothurians the young ones are carried about embedded in the skin; in one of our British starfishes the young ones, which are in this case like miniatures of the parent, may be seen clambering about on the outside of their mother's body and keeping firm hold as she moves—a very different kind of early development from that seen in most starfishes, which

have free-swimming pelagic larvæ. Now in these two cases there are no nerve ganglia at all, no more than strands and networks of nerve-cells and their fibres; and, in this absence of centralisation, it follows that we must, in our descriptions of the behaviour, avoid as far as possible any psychological implications. There is obviously an objective parental care, but of a subjective side there is almost as little hint as in a gooseberry-bush with its clustered fruits, or in a tiger-lily with the bulbils hidden in the axils of its leaves. We do not, of course, assert that the subjective side is absent in either case, but keeping to the verifiable data, we do not at present know anything about it. As there is an inborn predisposition or hereditarily determined prearrangement in the dog-whelk to make a protective

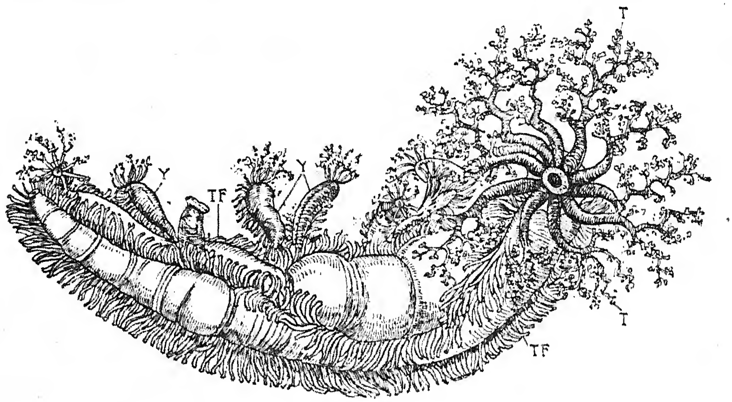


FIG. 84.

A Holothurian (*Cucumaria crocea*), with numerous young ones (Y) attached to the skin. After *Report of "Challenger" Expedition*. TF, locomotor tube-feet; T, tentacles.

capsule for its eggs, or in the trapdoor-spider to sink a shaft which secures their safety, or in a cuttlefish to fasten its egg-clusters among marine vegetation, or in a mosquito to make buoyant egg-rafts which cannot be sunk, so it is instinctive on the part of the brook-leech to carry its young ones on its under surface until they are able to fend for themselves. The fact is that near the commencement of the inclined plane of parental carefulness we have mostly to do with behaviour that is in the main the outcome of inborn or engrained instinctive promptings—part of the hereditary make-up.

At what level the parental care begins to be worthy of the name, acquiring an emotional tone, who can tell? It seems very unlikely that worker-bees, which nurse their mother's grubs so loyally, have more than a hint of awareness of what they are doing, or more than a hint of vicarious maternal emotion in their objeetively unsurpassable solicitude. When a mother Sphex wasp provisions the cradles

in which she deposits her eggs, working hard to capture suitable insect booty, which is then skilfully paralysed so that it remains fresh meat for the future larvæ, she cannot be credited with much feeling, for she never survives to see her hatched offspring. Her ancestors may have had this experience, but that must have been long ago. The whole routine has passed under the rule of instinct, and the exacting tyranny of this in the case of the Sphex wasp has been well illustrated by Fabre's famous experiments.

It seems reasonable to suggest that awareness of the offspring and enjoyment of their presence cannot be more than hinted at until the nervous system has attained a considerable degree of complexity, and until the offspring are nurtured by and sojourn with the parent for a considerable time. Only then is there a distinct sounding of the emotional note.

The instinctive basis of much of the parental carefulness of animals must be kept in mind even at the highest levels, for this unreasoning basis, on which intelligence may proceed to build, helps to explain some of the curious puzzles, so often provocative of misunderstanding on the naturalist's part. Hamerton tells of a bereaved cow which would not feed and would not be milked, and was like to die. So the farmer stuffed the calf's skin with hay and set it up before the mother, who recognised the smell, was comforted, licked the skin repeatedly, and began to mend. As she continued licking, she wore a hole in the calf's skin, and went on complacently to eat the hay!

Now we misunderstand the situation if we are led by this tale to depreciate either the cow's intelligence or its parental emotion, both of which are strongly developed. The smell and the touch of the faked calf served as a "liberating stimulus" towards health, and there was probably an associated emotional tonic. But the touch and taste of the hay liberated another instinct, and the cow ate contentedly, untroubled by any desire or need for a consistently unified experience. Animals seldom worry over discrepancies; that is man's affair.

Some of the grades of parental care may be mentioned, the proviso being understood that at the lower levels the behaviour is little more than an expression of the physiological arrangements embodied in the animal's constitution. A dogfish automatically produces in its oviduct an elegant mermaid's purse, whose tendrils twine automatically around seaweed or zoophytes, and thus save the developing embryo from injury. But there is no reason to suppose that the dogfish is more aware of the adaptive arrangement than a plant is aware of the equipment of its seeds with some structure that secures their dissemination.

(1) The eggs and developing offspring may be carried about in various ways by the parent, e.g. in a brood-chamber in many small crustaceans, or on the surface of the body, as in the brook-leech.

(2) There may be some manipulation which secures the attachment of the eggs and developing offspring to the parent. Thus some mother-spiders fashion a silken bag or cocoon around the eggs and attach this by threads to the under side of the body.

(3) In other cases the care is expressed in hiding the eggs and developing offspring. This may be a very simple matter, as when a snail drops its eggs into a hole in the ground, but it may have considerable finesse, as when a sawfly bores a hole in wood and deftly inserts an egg.

(4) The hiding of the egg in a safe and suitable place often reaches a high level of "instinctive art", which may require prolonged manipulation. Thus the female trapdoor spiders make beautifully finished shafts (furnished, for instance, with hinged lids) which are shelters for the eggs and the young. Still more extraordinary is the

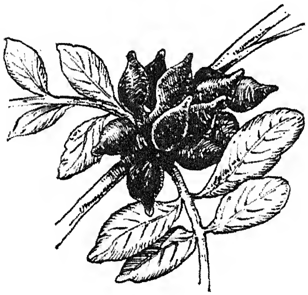


FIG. 85.

Bunch of Sepia Eggs, attached to a Shallow-water Marine Plant. After Jatta.

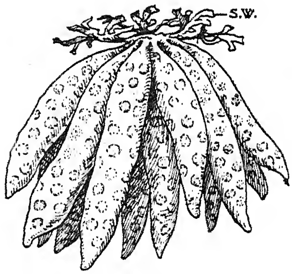


FIG. 86.

Egg-clusters of the Squid (Loligo), attached to a piece of seaweed.

silk nest which the Water Spider (*Argyroneta natans*) spins in the pool and fills with dry air. Its entire significance is in relation to the eggs and the young spiders.

(5) Another level is illustrated by those cases in which the mother animal remains near the hidden eggs and developing offspring, and may sometimes drive off intruders. Thus the Madagascar Crocodile lingers beside the eggs laid in the soft ground, and is ready to unearth the young ones when they are about to be hatched and pipe from within the egg-shells. The male stickleback defends the weed-nest which he has fashioned, in which the absentee female parents have deposited eggs.

(6) Rising out of the protective lingering beside the developing eggs are the various forms of brooding, which reaches its climax in birds. This may secure not only safety, but a more rapid and smoother development; and it should be kept in mind that it is the rule with migrant birds that they nest in the colder part of their migrational

range. For the parent bird there may be an advantage in safe resting after the reproductive strain, and in some cases it seems that the brooding is linked back to conjugal sex-relations for which the nest was the territorial centre. In hundreds of cases the male birds share in the brooding; in some instances, as in other forms of parental care, they assume the whole responsibility.

(6) Another note is struck when the offspring remain beside their parent or parents for a considerable time, receiving food, protection, and instruction.

(7) It seems useful to separate off the various expressions of viviparity, especially in the big-brained mammals, where the mother carries the unborn young for weeks or months, and even, in the case of the elephant, for a couple of years! Yet we must admit that the very careful nurture which a mother mammal often gives its offspring is to begin with on an instinctive basis, and it is an instructive warning against too generous psychology to notice that a ewe who has licked another's lamb may appropriate it, to the detriment—sometimes fatal—of its own, as yet unborn. An inexperienced cow, excited after delivery, may kill its newborn calf, which alarms it by a sudden movement of its head. But when smell and taste have served as the liberating stimuli of the instinctive routine, no mother is more objectively devoted and maternal emotion shines through her eyes.

The highest expressions of parental care are to be found in those cases where the offspring remain for a long time under the protection and tutelage of the mother, or of both parents, and there is more than a beginning of family life.

INSTINCT AND INTELLIGENCE.—As it seems to us, a misunderstanding is apt to arise, even among experienced naturalists, when instinctive and intelligent behaviour occur side by side in one and the same animal, yet without the capacity for judgment or inference (*intelligence*) being able to help the inborn chain of reflexes and their correlated psychical side (*instinct*). Among the experiments made with pigeons by the late Prof. Whitman, there were several which took the form of removing the eggs from the nest during the brooding bird's absence and leaving them in the immediate vicinity, within reach of the nest. When the bird returned, she was apparently more influenced by the sight of the nest than by the sight of the eggs, and, in some cases, she ignored the eggs altogether, though it would have been easy to retrieve them. We interpret this by supposing that the whole business of brooding has passed so completely into the domain of the instinctive that it is not easy to awaken intelligence in this connection, though pigeons often have much. The behaviour of Whitman's pigeons varied notably according to the species or variety of bird, for some were less thirled to instinct

than others. A recent modification of the experiment by Mr. H. Guthrie-Smith consisted in putting the egg on the margin of the nest so that the bird's settling down made it move a little inwards. That movement, or perhaps the contact, seemed to pull some trigger, perhaps of an instinct to sit on the eggs and not merely upon the nest, for the bird proceeded to adjust her body until the egg was moved into its proper place, where it could be effectively incubated. More experiments with what is sometimes mistakenly called "the hopelessly stupid" might throw some further light on the contrast between instinctive and intelligent behaviour.

EDUCATION IN ANIMALS.—In some birds and mammals it has been observed that the young receive parental education. This varies in its detail in different cases, for it may be little more than the supplying of a liberating stimulus or an incentive to action, while in more complicated expressions the education amounts to careful training in the way in which certain things should be done. The parental instruction is advantageous in lessening the time required if dexterity has to be learned by individual experiment. It also lessens the risks of the self-educating method. Moreover, in all probability, there is some profitable handing-on of the gains of parental experience—a simple form of extra-organismal heritage.

To begin with simple cases, we may notice how a dabchick, with its young ones on its back, depresses itself in the water and thus forces them to begin to learn to find their way about. A grebe has been seen ducking one of its offspring, as if accustoming it to immersion. The Great Crested Grebe often dives after fish while carrying the young ones on its back, and they soon learn their lesson. Although young birds do not require to be taught to fly, the parents may force or encourage them to make a beginning, sometimes tempting them with food. A guillemot may push its young one off the brooding ledge on to a slope which leads steeply to the sea. Mr. Coward notes that "a more usual method is for the old bird to seize the unfortunate by one wing, and, flying out with it until clear of surf and rocks, let it drop". The young bird opens its wings and flutters. It takes its first flight diagonally down to the sea, where it also takes its first, somewhat compulsory, dive, and follows this by beginning to swim. It is waited on by its parents, or by one of them, and gets some help with its meals until it is able to fend for itself. There are several similar cases well documented.

Some forms of education take the form of graduated meals, as has been observed in birds of prey, like the Peregrine Falcon and the Golden Eagle. From carefully prepared pieces of flesh, to begin with, the nestlings are gradually trained to tackle more or less intact booty. L. T. Hobhouse refers to the expertness shown by some young woodpeckers in getting at the seeds of fir-cones, but he points

out that the parent woodpeckers bring their young ones first the seeds themselves, then partly opened cones, and finally intact ones. "The method of preparing the family dinner is at least as much a tradition as an instinct." It is the outcome of both teaching and learning.

Among mammals the instruction is almost always on the mother's part. The carnivore often brings a living captive to the den and sets it free in presence of the young ones. This serves as a liberating stimulus to instinctive capacities, but it also affords some training. In many cases, e.g. foxes and stoats, the mother takes her offspring with her on her hunting expeditions, and they gradually learn their business. The instinctive basis is of course present, but its exercise under maternal control may continue for months. Tregarthen describes circumstantially the detailed instruction given by the mother otter to her cubs. It includes the long alphabet of country-sounds, the fit and proper ways of diving and lying *perdu*, the methods of capturing different kinds of booty, and the recognised ways of eating trout, eel, and frog. It may be safely said that too little attention has been given to the factor of education in developing animal behaviour.

Different Forms of Family.—There are various forms of family life among animals, all of them of interest to man. In many cases, of course, although there is an abundant progeny, there is no family. This is evidently the case with those fishes that spawn somewhat fortuitously in the water, and have not even a beginning of parental care. Similarly in frogs, the spawn in the ditch is left to itself, and the tadpoles that hatch out from a clump of eggs do not remain together in any systematic way. If they did, it would be the beginning of a filial, though not of a parental family. In general it may be said that animals which illustrate the spawning method of multiplication do not show any family life. The starfish Luidia, which is credited with producing 200,000,000 of eggs in a year, could hardly be expected to have a family circle, and yet we have seen Müller's starfish (*Asterias muelleri*) with the young ones clambering about on the body of the mother. This marks a stage in the formation of a parental family.

The typical parental family is that in which both parents remain for some time in helpful company with their offspring. One of the highest expressions is seen, according to Reichenow's observations, in a band of twenty or thirty gorillas, where there may be five families—each of father and mother and a number of children. A pretty case among birds is that of the common wren, where both parents share in the family duties, and may utilise the old nest as a shelter in the winter nights, not for themselves alone, but for a number of their offspring as well. In spite of Seebohm's vigorous

criticism there seems to be no doubt that there is often gregarious roosting in winter; and where the shelter is the old nest it is difficult to hesitate in regarding the little group as a family party. If this is the case, it is a simple extension of the family life beyond the breeding season. In some species of ducks and geese the young birds remain for the greater part of a year under the protection and tutelage of their parents. Even in such pronouncedly predatory mammals as the lion and the fox, the father stands by the mother and the family for a long time, helping not only in defence, but in providing food. At a much lower level in a few pioneer fishes we find indications of the beginning of a bi-parental family. Thus in some of the wrasses (Labrus) both parents make a nest of seaweed and zoophyte, pieces of shell and debris, and both share in the protection of the eggs and

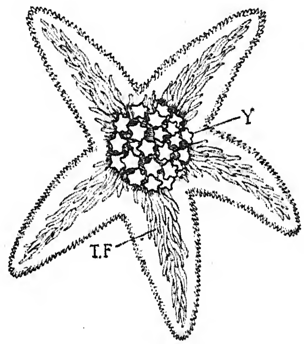


FIG. 87.

A Starfish (*Asterias mülleri*), showing parental "care". A cluster of young ones (Y), which have suppressed the usual pelagic larval stage, are seen attached on the under surface of the mother. TF, tube-feet.

the offspring. Prof. Doflein reports the interesting case of a fish called Eupomotis, where both parents share in building and watching the nest, to which the young ones return every evening for three weeks after hatching.

The second kind of family is maternal, where the mother takes sole charge. Thus the female spider may not only carry the developing eggs in a silken bag, which she will defend to the death, but she sometimes bears the hatched spiderlings on her back till they are able to fend for themselves. One must of course distinguish parental care from parental family life, the distinctive note of the latter being that the offspring remain for some time externally associated with the parent or parents, from which they derive some assistance. A mother-spider has been seen feeding her young ones with flies, but this is very unusual!

A hen with her chickens is a good example of a maternal family under man's shield, but the same sight is common in Wild Nature

among polygamous birds. Small herds of eight or so elephants seem to consist, in some cases at least, of a mother and her children, whose births have been well spaced out over many years. A mother marsupial with her young ones in her pocket, or on her back, illustrates a quaintly simple form of maternal family; and we can follow this into simpler and simpler expressions down to cases like the hermaphrodite brook-leech, which carries its young ones on the under side of its body. We must again lay emphasis on the difference between parental care before birth and helpful association afterwards; thus, when certain mother Cichlid fishes hatch their few eggs in their mouth, that is remarkable maternal care; but when as in some of these fishes (allied to wrasses), the hatched young ones swim about around their mother and return to her mouth when they are in danger, that is a simple instance of a maternal family. Some of the illustrations are startling; thus it is reported of certain kinds of scorpions that they catch insects for their offspring, and even prepare the food by tearing it into small pieces.

The third kind of family is paternal, where the father takes sole charge. Thus the male stickleback makes a nest and defends it, and passes from father to patriarch as he looks after the brood until they are able to be left to themselves. When they stray prematurely he brings them back to safety, thus striking a very distinct family note. It is well known that a number of male fishes take charge of the eggs, the Sea-horse in his breast-pocket, the Kurtus on the top of his head, and the Gaff-topsail in his mouth—which means fasting for two months; but these and other equally strange cases are illustrations of nothing beyond paternal care. The family note begins to be struck when the male of the fish called Arius not only incubates the eggs in his mouth, which seems a little like tempting Providence, but, after the hatched young ones sally forth, opens his jaws for them to return when danger is imminent. Better a father's jaws than a stranger's!

One likes the story of the American Amia or Bow-fin, where the male mounts guard over a rough-and-ready "nest" that has been cleared among the water-weeds. After the young are hatched out they leave their cradle in a body, and their proud father goes with them. He circles round the swarm like a collie round a flock of sheep, and they remain under his watchful eye and solicitous protection for about four months. This is family life.

Strangest of all is the behaviour of the male Rainbow Fish, Trichogaster, who makes a floating island of pieces of water-weed, buoyed up with bubbles of air. He injects the bubbles of air so deftly that the centre of the little island is swollen up like an open umbrella. Under this canopy he brings the female, whom he has diligently courted, and she liberates the eggs so that they float up under the bubble-nest. The male not only guards the nest, but keeps

it in repair by adjusting the weed and by blowing in more bubbles. If a water-snail intrudes, who would devour the developing eggs, he drives it away; if an egg falls out he picks it up and blows it back into shelter. When the helpless fry are hatched out, he continues to look after them. How altruistic the whole behaviour of the male bubble-nest fish, but why is he so keen that the mother shall have none of the credit? We ask this, and the beautiful bubble bursts, for in aquaria at least, when the young ones begin to move about actively, the lately "altruistic" father is the first to make them his prey.

In mankind we know of matriarchal and patriarchal families—or at least matrilinear and patrilinear—and of the modern type where the two parents count more equally; but there is a fourth kind of family, which only animals could illustrate. It is explained by Alverdes in his recent book on animal sociology, to which we are much indebted. It is the children family, and it is said to be illustrated at various levels, e.g. by reindeer, certain kinds of whales, some of the pythons, certain fishes like herring, and some caterpillars like those that form processions. But these combinations of youngsters of the same age may be ranked as incipient societies rather than as families.

Monogamous Animals.—Many fishes multiply in a very automatic way, without almost any relations between the sexes. The personal touch is practically a-wanting; for the eggs are shed from the ripe ovaries or roe, the sperms making the milt are similarly shed by the males, and fertilisation takes place fortuitously in the water. In most cases all that can be said is that the presence or the spawning of the one sex serves as a stimulus to the other. Very gradually, however, in a minority of cases the personal touch has evolved. That is to say, it is possible to make a series from the mere contact of males and females up to elaborate courtship. Two pipe-fishes may twine their bodies together; in sharks and skates there is internal fertilisation; and from such simple beginnings of personal relations there is an inclined plane leading to the elaborate ongoings of sticklebacks and bubble-nest fishes. In one of the South American cat-fishes there is a prolonged courtship, then an embrace, and then a hiding of the fertilised eggs in a safe corner.

There is an interesting little fish called the Bitterling that lays its eggs in the gill-plate of the freshwater mussel. It is a gregarious fish; but at the breeding season the individuals separate in pairs, coming together again when the sex-urge is past and hunger is once more the ruling passion. This is what might be called seasonal monogamy. Thus two scarabee beetles live as mates for the season and help one another to make and roll the balls of dung which serve as stores of food both for themselves and for their offspring.

The male and female water-spiders seem to keep company and their tempers all the summer through, which is more than can be said of most of their kindred. The case of Darwin's frog (*Rhinoderma darwini*) is very quaint, for the female lays eggs singly or in pairs, at intervals of several days, and after the male has fertilised them he stows them away in a croaking sac. He is said to be contentedly monogamous, and perhaps this is not surprising when parental is spelt paternal. Many birds are loyal mates for the season, but may form other unions another year. Changes are lightsome, and the problem of giving the family a good send-off is solved for each successive year. For many mammals the same is true; they are seasonally monogamous. This holds for lions and jaguars, while foxes and bears show an interesting extension of the marital companionship beyond the limits of the breeding season. Reynard the Fox sometimes protects his playful children—who could resist them?—and brings them food. The same is true of wolves, yet everyone knows that they become a pack in winter.

But there may also be seasonal polygamy, which differs from permanent polygamy, inasmuch as the association breaks up after the breeding season is over. This is the case with many ruminants, such as cattle, deer, and antelopes. There is a harem, more or less loyal to a single male; but it is not likely to be the same male a second season. In some cases, such as elephants, the situation is complicated by the fact that there is a single female at the head of the harem; and perhaps she has more power than the lord and master of them all. Yet another complication is seen when there is seasonal sex-association, either monogamous or polygamous, within a herd or community. It is monogamous among marmots, prairie-dogs, and white whales; it is polygamous among most of the seals.

Many animals have risen to the level of personal relations, but linger at the stage of promiscuity. Any mature female may surrender to any mature male. Any ripe male may be amorously excited by any ripe female. These relations are above the level of automatic spawning and fortuitous fertilisation, but they are promiscuous and transient. Thus frogs pair and part; and though the croaking of the males is a sex-call, there is no individual reference. Any female for any male is the rule. The same promiscuity is illustrated by many of the gregarious lizards, by such birds as ruffs and cow-birds, by such mammals as hares and bats. The distinctive feature is not that a male has to do with several females, or a female with several males, for this would be true of polygamy and polyandry, but rather that there is pairing without mating. There is little more or no more than a transient sex-encounter. There is no "marriage". But in all these matters it must be recognised that there are no hard-and-fast lines. The roving hare has no doubt a psychical side to his passion,

and a light-o'-love lizard may linger beside his mate after the physiological storm has passed. Very gradually there is an ascent to cases where the marriage, if we dare use the word, lasts for a season or for life.

In many birds, where æsthetic courtship reaches a very high level, the sex-urge is sharply punctuated. It is intense while it lasts, but it does not last long. The reproductive organs soon begin to dwindle, and the bodily excitement wanes; the hormones or chemical messengers from the gonads cease to be made and distributed in anything like the same degree; the whole life becomes quieter and more commonplace. Thus even at a high level there may be seasonal mating which is automatically dissolved when the sex-urge sinks for the time being into quiescence. In some short-lived animals there is only one love season in the lifetime.

What seems to man the highest level of sex-association is permanent mating; and this may be evolved on polygamous or on monogamous lines. Thus in the case of the South American Ostrich, the Rhea or Nandu, the troop consists of a male with half a dozen or so hens. It is a lasting association, persisting even when troop joins with troop outside the breeding season. The females of a troop pool their eggs, or as many of them as possible, and the male-bird broods. The young birds follow their father at first, but the mothers gradually insinuate themselves. Among the guanacos and vicunas, the wild ancestors of alpacas and llamas, there are permanent troops, a male and a harem; and so it is with wild horses and zebras, kangaroos and macaque monkeys. There may be a large herd of wild horses or a large community of monkeys, within which there are permanent polygamous, or, better, polygynous, groups—each consisting of one male and several females.

Solitary monogamy is characteristic of many birds, such as eagles, ravens, cranes, storks, and swans. It is of course difficult to be always sure that the two birds are the same year after year, but in some cases this has been securely proved. There is the same difficulty with wild mammals who live in pairs; for marking is even more difficult than with birds, but there are instances that seem reliable, such as rhinoceros and orang. Monogamy within a herd or community is illustrated by some gorillas and chimpanzees, just as by penguins and parrots among birds. In some cases the monogamy is loosely observed, especially on the male's part, as is well known for sparrows and rabbits; in many cases, however, the lifelong monogamy is strict and is loyally respected. It is an arrangement that works well for the family, but a little consideration shows that this is not its chief significance in the animal world. For the welfare of the family is satisfactorily secured by other arrangements besides those of monogamy. The true inwardness of lifelong monogamy is deeper. Mating for life means that psychical love has prevailed over physical

fondness; psychical chains have been forged which bind the mates together as willing captives to one another. The beating heart of monogamy is the love of mates. So in these times, when our traditional human pairings are being so widely criticised, and even so boldly relaxed, must not the evolutionary naturalist put in the warning word—beware of reversions!

Male Parents Mothering the Offspring.—At various levels among animals the parental care has become altogether *paternal*. This is true of a few birds like the American Ostrich or Rhea, where the male does all the brooding and afterwards leads the young ones about. In the Grey Phalarope, that nests in Greenland and Iceland, the more brightly coloured female does all the courting and the male does most of the brooding; in the Red-necked Phalarope, that nests as far south as the Orkneys and Shetlands, the female again does most of the courting and the male most of the brooding and nurture. The exceptional exchange of roles is completed when the female mounts guard over the brooding male!

It is the male stickleback who builds the nest, binding the parts together with threads exuded from his kidneys. The little polygynist brings the nonchalant females to his neat construction, in which each lays a few eggs and departs, careless of either conjugal or parental responsibilities. Then he mounts guard over the fertilised eggs, driving away enemies, eating nothing all the time. When the eggs hatch and the living marks of interrogation come out, he still watches over them, trying to keep them within bounds. The male stickleback is a motherly father!

The quaint nurse-toads or obstetric toads of the Continent pair on land, not, like ordinary frogs, in water. The female liberates a string of 18–38 eggs, and the male gets this attached to his hind legs. For a time he keeps in private life, hiding himself in a damp hole. Occasionally he ventures into a pool for a bathe. The eggs go on developing, still attached to his legs. Tadpoles are formed within the egg-membrane, and there they pass through the stage with the first or external set of gills. When they reach the stage with the second or internal set of gills, the father-toad jumps into the water. Then the egg-membranes are burst, and the tadpoles swim away. The male is freed from his living shackles, and not very unlike shackles they are. He creeps on to land again, and long afterwards his family do the same. For the period of infancy this nurse-toad is a motherly father!

One would like to have a more intimate knowledge of the strange animals called sea-spiders or Pycnogons, which are represented by many kinds, from the shore to the great depths. For the eggs liberated by the female are carried by the male, attached in two bunches to the third pair of appendages. The corresponding limbs

in the female are sometimes vestigial, sometimes absent, so it looks as if the habit was one of long standing. Can it be that the females die, or are seriously exhausted after producing the eggs, and that a division of labour has been worked out whereby the males discharge all the parental functions except the actual egg-production? But no one seems to be able to tell us whether the mother sea-spiders are short-lived or not. Or is it possible—we clutch in our ignorance at straws—that the attached eggs serve as a continued sex-stimulus to the males? In any case it is a very remarkable sight to see a large long-limbed male sea-spider from the depths of the sea bearing not merely big bunches of eggs, but sometimes a host of fully-formed young ones clambering about over his body and limbs. It gives one a new impression of the possibilities of paternity.

A volume might be written on the subject of paternal care. Picture the father hornbill working himself to a skeleton, sometimes

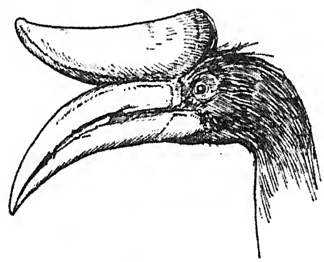


FIG. 88.

Head of Hornbill (Buceros), showing an exaggerated growth of bone forming in both sexes a remarkable helmet or casque on the upper surface of the skull. Its use, if any, is unknown.

to death, to provide food for his spouse and small family, immured in a hollow tree. All the hard work falls on him; he has not a minute to himself! And though the tale turns out not to be true that the eider-drake allows his breast to be plucked by the eider-duck, in order to make a new quilt for the nest, to replace what man has stolen, there is too little appreciation of the part so many cock-birds take in building the nest, in brooding on the eggs (surely at first the mother's duty), in bringing food to the young, and sometimes even in providing musical entertainment while the hen simply sits. And conversely there is no adequate recognition, for instance, of the courage with which a goose will defend the goslings against enemies, as a cow her calf.

To take another instance, the male lumpsucker fish (*Cyclopterus lumpus*) mounts guard over the curiously big bunch of eggs which the female has spawned in the recess of a shore-pool at low-tide. He remains there, fasting, we believe, and not only defending the eggs from intruders, but aërating them with squirts of water from

his gill-covers, or washing off mud with energetic strokes of his tail. Some male fishes like the Cichlids put the eggs in their mouth, so that they may be quite safe. This is going a long way. Very well known is the pocket of the male sea-horse, so attractive an inmate of every large marine aquarium. When the eggs are liberated by the female, they are received into the skin-pouch formed on the ventral surface of the male; and there they are carried until the young ones hatch out. What a motherly father is the sea-horse!

Apart, perhaps, from Darwin's little frog (*Rhinoderma darwini*),

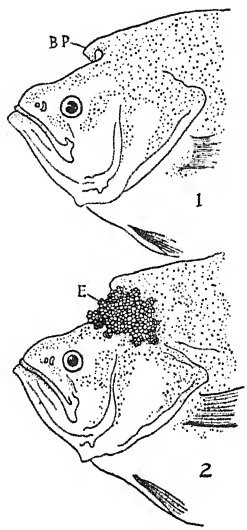


FIG. 89.

The Head of the New Guinea Fish, Kurtus (*after* Weber). The upper figure (1) shows the growth of the bony process (BP), forming a hook. The lower figure (2) shows the bunch of eggs (E) fastened in the hook, which has become a ring.

which is original enough to cradle the eggs in his croaking sacs, the case of Kurtus appeals to us most. In this New Guinea freshwater fish the male develops at the breeding season a bony process on the top of his skull, which grows forwards and downwards like a bent little finger. The eggs are few in number, and they are entangled by enveloping filaments in a floating double clump, like a double bunch of grapes. The male butts against the eggs and gets them under the process on his skull just before its hook becomes an eye. So he carries them about on the top of his head until the young ones emerge. A case like this makes one doubt whether there is not some missing psychological factor in our customary treatment of organic evolution.

What can one say of these motherly fathers? In the first place, sex is not a crisply defined character, there are masculoid females and feminoid males. Masculine characters lie latent in many females, as in birds; and a male mammal may be made to give milk; it seems even that this has appeared in Man. Parental care, likewise, is not wholly maternal; egg-care is not a monopoly of the mothers. Variations are frequent, and, should it become necessary, it is open to males to become motherly. In any case, by capping the stories of "parasitic males" with those of motherly fathers we may restore a more balanced view of Animate Nature.

In the second place, the reproductive sacrifice is greater in the females, and the mother animal may die after reproduction. Then if parental care is necessary the only possibility of survival is that the males should become motherly.

All such cases as the above are also of interest towards bringing out more and more of the manifold analogies between animal and human behaviour. So is it not a pity that the great fabulists from Pilpay and Esop to La Fontaine, and again to Uncle Remus, did not know such stories? For what parables for parents would they not have given us, and this not only with appreciation for fatherhood at its occasional best, but even towards its more general bettering! Indeed, do not widowers often show this?

THE ARGONAUT'S CRADLE.—Few naturalists have had the pleasure of watching the female paper nautilus or argonaut in an aquarium as Mr. Beebe did on the *Arcturus*. She was in an explosive temper when she was put into the tank, and effaced herself in a cloud of sepia. Indeed, she had to be transferred twice before she had emptied her ink-bag and could be clearly seen. "She rested quietly on the bottom with her many arms wrapped about her beautiful brown and white shell. But, as soon as my face approached the glass she rushed back and forth shooting directly at me, or bumping against the opposite glass, and, finally, backing into a corner." She eventually condescended somewhat ungraciously to accept a small fish, which she ate. In all probability, some parental complex made her furious, for, two days later, in a paroxysm of rage, she flung herself clear out of the shell, which, is, of course, rather a cradle than a house. It is not represented at all in the much smaller male, and, instead of being secreted by the "mantle" as in other molluscs, it is made by two flat plates on two of the arms—the two arms which some of the old naturalists believed she held aloft as sails to catch the wind. Mr. Beebe found thirteen hundred eggs in the shell, each about ten millimetres by fifteen, tied loosely together like miniature bunches of grapes. Some of them were well advanced in development, and showed the embryo argonauts with two relatively large red eyes.

THE POSITION OF WOMAN: BIOLOGICALLY CONSIDERED

THE BIOLOGICAL ASPECT.—The position of woman, or that of man, may be considered from many points of view—politically, economically, ethically, and so on. Here our point of view is, of course, *biological*; that is to say, man and woman are discussed under the category of "organisms". They are studied as one would study peacock and peahen, ruff and reeve, stag and hind, lion and lioness—as creatures of flesh and blood, with characteristics that can be measured. It need hardly be said that in a short section, we cannot do more than give a few *illustrations* of the biological mode of inquiry, leaving human considerations till later.

The biological point of view is indispensable and fundamental—simply because we are creatures of flesh and blood, but it is as obviously partial, requiring to be supplemented by other considerations which we may justly call supreme, since they have to do with our rational and social life. This admission is continually made by biological investigators of mankind, and it is therefore neither generous nor useful to taunt them with their "breeder's point of view". Nor is the taunt accurate, since the biological point of view is wider than the breeder's, and considers the whole organism and its whole life. It is even wider than the *medical* point of view, for although medicine is to some extent applied biology, the science has a larger scope than the art. Biology has mostly to do with what is *normal*, and it concerns itself not with individual persons, but with averages, or rather norms.

SEX-DIMORPHISM.—In contemplating Man and Woman with their specific resemblances, and with their hundred and one differences, biologists have before them what is familiar in the higher reaches of animal evolution—namely, sex-dimorphism. No one without a microscope can tell a male from a female sea-urchin, and in the lower reaches of the animal kingdom an external uniformity of the two sexes is very common. As we ascend the series, however, dimorphism becomes more and more frequent and conspicuous. The essential functions of males and females become more and more different, their habits of life diverge, and to the primary differences there are added all manner of secondary peculiarities. Yet there are many birds and mammals in which the two sexes are practically identical except as regards the reproductive system.

Walking warily—since the difficulties and uncertainties are very great—we hold to the view that there is a deep constitutional difference between the male and the female organism—an initial difference in the balance of biochemical changes. The female seems to be relatively more constructive, relatively less disruptive. There

is a fundamental difference in physiological gearing. This initial difference leads to the primary functional distinction between male and female. But it also determines, either from the start, or after maleness and femaleness have been established, what particular expression will be given to a whole series of minor characters, both structural and functional—whether a masculine or a feminine expression.

We must refer to the section on Sex-Determination for some of the evidence in support of this view—that a deep, initial, constitutional difference expresses itself primarily in what we may call maleness or femaleness, and is also decisive, late or early, directly or indirectly, in determining whether detailed characters will find a masculine or a feminine expression.

In some cases, probably, the initial difference is itself continued on in the building up of every part, deciding, as it were, at point after point whether the hereditary characters will express themselves in the masculine or in the feminine mode. In other cases, certainly, it is the saturating influence of the early established maleness or femaleness that determines the development of detailed parts, and of habits as well as structure. In Vertebrate types this activating of masculine or of feminine features is often under the control of the hormones which are liberated into the blood from the developing reproductive organs or gonads.

It is important to realise the saturating influence of primary maleness or femaleness, as the case may be. The sex-dimorphism is pervasive, it goes through and through. As Havelock Ellis says, "A man is a man to his very thumbs, and a woman is a woman down to her little toes." The difference can be read in the blood—so safe and subtle an index to what goes on throughout the body. The difference can be read throughout life—it is seen in the baby boy and baby girl, it is expressed in old age. Of the more technical evidence we give only one illustration. A castrated pullet may acquire not only the outward structural features of the opposite sex—cock's comb, wattles, long hackle and tail feathers, rapidly developing spurs, carriage, etc., but the behaviour as well, even to the pugnacious character.

It is also important to realise that masculinity and femininity differ much in their accentuation. Thus, to recall but one instance, the female of the Red-necked Phalarope is a perfect female, but she is extraordinarily masculine; her mate is a perfect male, but he is very feminine.

The practical utility of this way of looking at things is obvious. It suggests that the characteristic masculine and feminine features are part and parcel of the normal man and woman, deeply rooted, not tacked on, of ancient origin and therefore not likely to change quickly. It suggests that they have a deep naturalness, and that

attempts to minimise them are very unlikely to spell progress. It suggests that while the expressions of the deep constitutional distinction are various in value—some trivial and some important—they are correlated, they hang together. To change the metaphor, the particular streams of femininity have the like origin as the rivulet which bears the developing embryo into femaleness.

Though as yet there is no unanimous finding of the biological court in regard to the essential nature of the constitutional distinction between male and female, some approximation to certainty and unanimity has been reached in studying its detailed expressions. We have said that the fundamental distinction crops out in every corner and penetrates into every recess, and its detailed expressions can be measured. It is here that precise science begins; but it has not more than begun. We cannot do more than single out some of the representative data which seem to be instructive.

As everyone knows, there is a whole series of anatomical facts which support the generalisation that in certain respects man's body is more specialised, going farther away from the youthful and primitive type. This cannot be explained away as wholly due to difference in activities. It is partly connected with the fact that man is longer of reaching maturity.

Ranke notes that the typical female form has a relatively longer trunk, shorter arms, legs, hands and feet; relatively to the short upper arms, still shorter forearms; and relatively to the short thighs, still shorter lower legs; and relatively to the whole short upper extremity, a still shorter lower extremity—and so on. In short, the woman is a less muscular, less motor type, in some ways more babe-like, in other ways more permanently adolescent.

What is suggested anatomically is corroborated physiologically; for tests show that the muscular strength of men is greater than that of women. This is borne out by careful experiments made between men and women physically trained, and of equal size and age. But caution is suggested by many observations. The rapidity with which little Japanese women will coal a vessel is said to be unsurpassable by men. Some of the bygone feats of Newhaven fishwives, carrying heavy creels for many miles, were extraordinary. Yet, to cite the quick collapse of a big strong man, who tries to help his little wife in carrying the sick baby about for a night or two, is just as useless as to point out that railway porters and engine-drivers are never women. On the whole, it seems safe to say that man is the more muscular type, and especially stronger in relation to isolated feats and spasmodic efforts.

Probably correlated and probably in part of similar deep origin is the quality often called "energy"—the characteristic masculine restlessness. Very hesitatingly we may perhaps go so far as to speak of woman's constitution and temper as more conservative, of man's

as more unstable. Man is perhaps more given to experiment both with his body and his mind, and with other people. In this connection we notice that there is among men a greater frequency of genius, insanity, idiocy, crime, and many kinds of anomalies. Stammering is much less frequent among females.

The physiologists tell us that man uses more oxygen and more combustible material, and has more waste in consequence. Man's blood has a higher specific gravity, more red blood corpuscles, more hæmoglobin. In short, man is the relatively more active or katabolic type.

Of some significance, again, is the relatively great tenacity of life in women. They are longer-lived. Alike in infancy and in old age they show a greater power of resisting death. Indeed, at every age, except 15 to 20, their tenacity of life is greater than man's. Their constitution has staying qualities, probably wrapped up with femaleness.

We have said enough to *illustrate* the detailed differences between man and woman, but we must briefly allude to three general impressions which we gain from the inquiry. The first is that the differences are correlated; they hang together, they are outcrops of the deep fundamental distinction. We may say that the tenacity of life, the longer life, the characteristic endurance, the greater resistance to disease, the smaller percentage of genius, insanity, idiocy, suicide, and crime, and so on, are all correlated with the distinctively female constitution, which may be theoretically regarded as relatively more constructive in its metabolism.

This correlation of differences includes the mental as well as the bodily, for it is impossible to separate them. We may assert this on general grounds which lead us to recognise the unity of the organism; but it can also be proved, in indirect ways at least. Thus Karl Pearson has shown that the inheritance of well-defined psychical characters can be formulated like that of physical characters. "We inherit our parents' tempers, our parents' conscientiousness, shyness, and ability, as we inherit their stature, forearm, and span." The psychical characters are inherited in the same way, and at the same rate as the physical.

To be carefully guarded against is the temptation to sum up the contrast of the sexes in epigrams. Personally we regard woman as the relatively more anabolic organism, man as the relatively more katabolic; and whether this biological hypothesis is or is not sound, it certainly does no social harm. But when investigators say that woman is more infantile and man more senile; that woman is "undeveloped man", and man an evolved woman, we get among generalisations not only extreme but practically dangerous. Not least dangerous of these generalisations is one of the most familiar that man is more variable than woman, that the raw materials of

evolution make their appearance in greatest abundance in man. There seems to be no secure basis for this generalisation; it seems doubtful whether any generalisation of the kind is yet feasible. Karl Pearson made seventeen groups of measurements of different parts of the body: in eleven groups the female is more variable than the male, and in six the male is more variable than the female. Moreover, the differences of variability are slight, less than those between members of the same race living in different conditions. Furthermore, an elementary remark must be permitted. Since inheritance is biparental, and since variation means some peculiarity in the inheritance, a greater variability in men, if true, would not mean that men as such had any credit for varying. The stimulus to variation may have come from the mother as well as from the father. If proved, it would only mean that the male constitution gives free play to the expression of variations, which are kept latent in the female constitution. What is probably true is that some variations find expression more readily in man, and others more readily in woman.

In regard to the mental differences between men and women we must from the biological point of view confess to feeling the difficulty of making definite statements until more experiments are accumulated, and the difficulty of distinguishing between extrinsic acquired differences and intrinsic innate differences.

It has been said that men have greater cerebral variability and more originality, while women have greater stability and more common sense. It has been said that woman has the greater integrating intelligence, while man is stronger in differentiation. "The feminine passivity is expressed in greater patience, more open-mindedness, greater appreciation of subtle details, and consequently what we call more rapid intuition. The masculine activity tends to a greater power of maximum effort, of scientific insight, of cerebral experiment with impressions, and is associated with an unobservant or impatient disregard of minute details, but with a stronger grasp of generalities."

But these are somewhat impressionist generalisations. What we require is a great extension of experiments like those of Miss Helen B. Thompson. She found that the ability to make very delicate and minutely controlled movements was slightly better in men-students. But may not this be connected with the greater use of knives and other tools? Ability to co-ordinate movements rapidly to unforeseen stimuli was clearly better in women. Women-students showed a greater power of distinguishing the higher and lower notes of the tuning-fork. But may this not be due to more early training in piano-playing or the like?

The eye of the man-student was on the whole more sensitive to light. The men perceived weak rays which were not seen by the

women. Can this have to do with more open-air life in the case of the men? The women distinguished colours better. But is this not the result of training?

Women showed, on the whole, a better memory; they learned by heart more easily and retained as well. They required rather less time for the association of ideas. The men showed a decided superiority in quickness of perception, as far as comparison could be made. In general mental content no differences could be established, not unnaturally, since all the subjects of the experiment had attended co-educational high schools in America.

A few experiments are of more value than many platitudes, but the basis is still too narrow for safe generalisation.

As to the tedious question of cranial capacity, it is difficult to believe much in the importance of slight quantitative differences—and, secondly, it is difficult to eliminate nurtural influences. Growth is inhibited or exaggerated according to the abundance of appropriate stimuli.

The great majority of the comparisons between men and women are vitiated by ignoring the familiar biological distinction between nurtural modifications and inborn variations. Through ignorance of the subject, or through inability to apprehend the biological point, many inquirers, who would also be teachers, have given support to anachronisms of opinion, which are nothing less than discreditable. Woman is set up against man, or man against woman, to the disadvantage of one or the other, without any handicapping committee, without the essential preliminary inquiry whether the opportunities of development, i.e., expression of the inheritance, have been even approximately equal.

It is indubitable that inherited characters require a succession of appropriate liberating stimuli if they are to develop. Supply these stimuli to boy and youth; deny them to girl and maiden; and then jeer because women make a formal muddle of a business meeting. Even in this matter, we omit to record the number of male meetings with formally lucid minutes, and the blackness of darkness in the actual result.

In comparing Man and Woman, it is necessary to try to discriminate between the innate qualities of maleness and femaleness, masculinity and femininity, all requiring appropriate liberating stimuli, and those which are individually acquired *as the direct result of peculiarities of Nurture.* Along with these must be included the defects that are due to disuse, or to the absence of appropriate stimuli.

Take one illustration: Long ago, Karl Vogt pointed out that women were awkward manipulators. Thomas answers well: "The awkwardness in manual manipulation shown by these girls was surely due to lack of practice. The fastest typewriter in the world

is to-day a woman; the record for roping steers (a feat depending on manual dexterity rather than physical force) is held by a woman; and anyone who has watched girls giving change before the pneumatic tubes in the great department stores about Christmas-time will experience the same wonder one feels on first seeing an expert shuffling cards! This consideration is extremely important in relation to mental ability."

The mind is in great part a social product. As Thomas puts it: "The mind and personality are largely built up from the outside, and if the suggestions are limited and particular, so will be the mind. . . . At present we seem justified in inferring that the differences in mental expression between men and women are no greater than they should be in view of the existing differences in opportunity."

First Proposition.—We have outlined the biological view that there is a deep constitutional or organic divergence between man and woman, and that this finds expression in a large number of detailed differences, which are natural in origin and natural also in being the outcome of ages of elimination and selection. Coming, now, to practical theses, we notice first of all that some of the educational, occupational, and social differentiations of man and woman in past times have been harmonious and consistent with the fundamental divergence. It seems consistent that men should fight, if there's fighting to be done; and that women should nurse, if there's nursing necessary. Man hunted and explored, woman made the home and brought up the children. Man sailed the seas, woman developed home industries. Woman is *naturally* a teacher of the young, a domesticator, a gardener, and so on. Scores of these harmonious differentiations still exist, and even develop, despite examples of the contrary.

This is an historical commonplace, which need not be elaborated; it suggests, however, several remarks that may be of service. (1) When we say that this or that occupational differentiation is natural to woman, we do not simply mean that it has been sanctioned by convention. We mean that it is congruent with femaleness, that it occurs in many races and countries, and that it has stood for a long time the test of eliminative selection.

(2) The harmless historical commonplace has sometimes been used in an obscurantist way to discourage the education of woman and the widening of her share in the world's work. "Her place is in the home", one is still told. To which one might answer much, but firstly, that much depends on the home. It was in very many-sided homes that woman evolved. And, secondly, that in the present condition of things, in this country for instance, a very large number never have what most men and women mean or should mean by a home.

(3) And, again, the historical commonplace has sometimes been used by those who are women's best, if not always wisest, friends. Some who have a firm grip of the fact that women are wives and mothers at heart, who are also influenced by the "technical education" fallacy of our day, have advocated a more predominantly domestic and maternal education for girls. But there are great dangers in exaggerating what in moderation is sound enough. A broadly educated, intellectually alert mother means much for the mental atmosphere of the home, and that means much for the children. And an over-emphasised domestic education is apt to force a premature development of mental and perhaps bodily instincts which, in many cases unfortunately, will find no realisation in life.

Second Proposition.—Our second thesis, the converse of the first, is that coercive differentiations inconsistent with the natural sex distinction have often been attempted, with unfortunate results. This mis-differentiation of women demands, like the harmonious differentiation, a careful historical survey, but we cannot give more than a few diagrammatic illustrations. Women have been used to draw the plough and to work in the mine; in some countries they are still employed as coal-heavers. Painfully often one still sees women bent and worn by physical tasks far too severe for them. Most of this is passing, but it is still necessary to say that the use of woman for functions which should be discharged by a beast of burden illustrates mis-differentiation. It is destructive of the individual; it is also prejudicial to the vigour of the race if it occur during the years of child-bearing and child-rearing.

A very different instance is that perversion of social sentiment which led to taking the veil being regarded as the highest devotion of a woman's life. Everyone recognises the beautiful significance of the step in particular cases, and the social utility of those who age after age have been truly the sisters of mercy; but this does not condone an ideal that renounced many of the most natural activities of woman, and involved an indubitable loss to the quality of the race by its segregation of many of its finest types.

But we do not require to go beyond the present for illustrations. Economic conditions are compelling women, in competition with men, into occupations and situations which are too hard for them, where the strain is too great, especially in adolescence, and where regularity of attendance is often so stringently enforced that health suffers. Where sex is ignored and where no allowance is made for maternity there is bound to be mis-differentiation. Where mothers are concerned it is certain that the wear and tear, the strain and continuity of the modern competitive system, whether in professional life or among hand-workers, must be prejudicial. As Karl Pearson says, "The race must degenerate if greater and greater stress be brought to force woman during years of child-bearing into active

and unlimited competition with man. Either a direct premium is placed upon childlessness, upon a crushing out of the maternal instinct on which the stability of society essentially depends, or woman has a double work to do in the world, and she can only do it at the cost of the future generation."

What to do is another matter, but we are mainly concerned just now in trying to see facts clearly from a particular point of view—to wit, biological. Much will depend on the growing organisation of woman-workers; much will depend on the developing social sentiment and the legislation to which that leads. In mediæval days a woman with child had certain privileges of game and fish from the lord's preserves, of gathering unhindered from field and orchard. This expressed a rough-and-ready social sentiment. Is it too much to hope that we may regain it and pass beyond it? For instance, is it too much to hope that an Education Department should welcome married women and mothers in the ranks of school-teachers, increasing the staff throughout, so that the necessary rests and long holidays should be granted when required, without stint or grudging? And, again, as Prof. Karl Pearson suggests, just as there are (in Germany at least) societies for insuring women against a possible spinster-poverty, so there is likely to arise a national insurance for motherhood. "The provision of such insurance", he says, "will for the first time allow of efficient regulation of the labour of married women during the child-bearing years—a regulation which will come none too soon to stop the degeneration of physique which is going on in certain classes of the labouring population." And as there is social sentiment that rewards the victims of war with glory and pensions, is it too much to hope for a progressive social sentiment which will equally reward the victims of maternity? One of the arguments used in defence of unequal political treatment of men and women is that men in the long run may be called upon to do what women cannot be expected to do—namely, fight. But against this stands the fact that men are not expected to bear children!

It may be said, however, that the incongruent differentiation to which we have referred is of less importance, seeing that most of the women-workers are unmarried. Of *less* importance, doubtless, but of great importance still. Not only in affecting the national expense of caring for invalids, but also in prejudicially affecting the prevalent feminine type—the significance of which may be realised without going deeply into social psychology. It must be remembered that although many of these girl-workers and women-workers remain unmarried, it is nevertheless from among their ranks that wives and mothers come.

It is, of course, obvious that it is not for amusement that girls and women strain themselves over tasks too hard for them. What

they do is an economic necessity. This is sadly true; but it is the biologist's business to insist on considering things biologically, not economically. Besides, everyone knows that the conditions of work are modifiable, and that they have been in many cases greatly improved. Moreover, it must be kept in mind that biological inefficiency is terribly expensive, and is itself cause as well as effect of social strain. Biological efficiency is the silver, at least, of our national wealth.

Here we may refer to the counter-thrust that one of the most obvious mis-differentiations of woman is that seen in the absurd attempts to over-educate her. Now this is much more than a jibe. For here we are confronted with the alleged relatively great infertility of types and stocks of high intellectual and social efficiency—for it is urged that the infertility is the nemesis of higher education and of individuation generally. Herbert Spencer argued that reproductivity decreases as individuation increases; and there is a considerable body of biological evidence in support of this generalisation. It must be observed, however, that we have no proof that high individuation *directly* lessens fertility. What the evidence from the animal kingdom shows is this, that when birds, for instance, were evolved with relatively big brains and strong parental care, it was possible to survive with very much smaller families. Those types that varied towards better brains and more parental care on the one hand, and towards economised reproductivity on the other, were naturally the survivors. But it was not necessarily the heightened individuation that *directly* lowered the rate of multiplication. It must be observed, also, that part of the reduced fertility may be due to hyper-nutrition and the like, to the frequent absence of love-marriages, to selfish celibacy and selfish non-maternity.

It is conceivable that the endeavour of self-realisation at a high level of culture may be so strenuous that it induces conditions tending against the making of good wives and mothers, but it can hardly be maintained that the deplored results are inevitable or intrinsically connected with the education. To admit that artificial and alterable conditions may tell against what the Germans call full motherhood and strong children is a very different matter from admitting that higher education for women is, biologically considered, bad for the race. Let us look into education later.

While one must keep on inquiring into a *possible* direct physiological connection between high individuation and low fertility, one need not make a bogy of what has not been proved.

Besides, we cannot but suspect that what is really wrong when individuation seems to be operating disadvantageously from the racial point of view is that the individuation is not all-round enough. One is apt sometimes to forget the splendid old grandmothers who were as able and intellectual and as highly individu-

ated as any one of their granddaughters, and what a lot of children, thank Heaven, many of them had.

This may be a fitting place for a reference to the interesting suggestion that the intellectuals among women should keep themselves free for work in the world which needs them so badly, and should leave it to their more placid, less ambitious, less intellectual sisters to be the wives and mothers. Those who admire the beehive will even point to it in support of their suggestion, for the queen-mother's brain certainly does not develop so well as that of the workers.

But the biological objection is just the same as against nunneries. It is sheer perversity to support a suggestion which deliberately leaves maternity to the less intellectual. And besides the clever mother's contribution to the organic inheritance of the child, there is the hardly less important nurtural influence in the home. The idea of leaving maternity to a docile and domesticated type of cow-like placidity, while the intellectuals run the world, is mischievously non-biological.

Third Proposition.—The third side of our thesis is that the lines of evolution to be followed are those which seem likely to make the most of the deeply rooted organic distinction between male and female, and to make the most of those masculine and feminine characteristics that have proved themselves for ages of vital value.

Taking a simple illustration first, we submit that Man—both male and female—is a very slowly varying organism, though he hides his persistence of type under ever-changing garments of acquirement and convention. In spite of affectation and pose there is still a wholesome abundance of that mutual attractiveness of complementaries which has given a spice to life from the beginning, and is of enormous biological importance. We venture to say that attempts to lessen the old-fashioned natural differences between the sexes are to be regarded with extreme suspicion. There is a wholesome natural prejudice against the masculine woman and the feminine man. What a resource of progress there is in sexual selection! How it will advance when economic conditions favour more discriminate preferential mating on the woman's part!

And if it be important that the culture of the body should be congruent with the fundamental distinction between male and female, and should make the most of the normal masculine and feminine attractions, the same is true in regard to the contrasted intellectual qualities, say, of mental experiment on the one hand and rapid intuitive insight on the other hand, or the contrasted moral qualities of, say, courage and affection. We have, perhaps, got away from the stupid anachronism of discussing the superiority of one sex or the other; but we have not sufficiently freed ourselves from obscurantism, since we are slow to act constructively, in

education for instance, in the way of making the most of the complementary sex-differences.

Thus, in the prolonged discussion over the pros and cons of co-education, how rarely has it been pointed out that no one method is ideal, for it is quite plain that boys and girls, men and women, should be taught together for certain reasons, and taught separately for certain other reasons. There are different studies and different modes of presentation for the two sexes if we are to make the most of their respective excellences. Of course, one may ridicule this position by asking for the masculine and feminine First Book of Euclid, and so on; though even here Mrs. Boole's mathematical lessons were very different from her husband's. Our point, however, is simply that if it were not for the expense we should have the sexes taught together *and* taught separately, taught by men *and* by women.

A professor of physiology in one of the largest American Universities explained to us that they were giving up mixed classes, and that he was heartily glad. On being asked for his reason he said that the women-students gradually lowered the standard of class-work, both of learning and teaching, and that it was in the interests of his men that he was stopping mixed classes. Such evidence is, or perhaps we may now say was, often used as an argument against the higher education of women, but there is a danger of taking too simple a view of these phenomena. The professor was giving a course of study specialised for the masculine intelligence; he was inhibited a little by the feminine element; there was no specialisation for the feminine intelligence; they were inhibited by this. In all probability he never got anything like the best out of them, and it is the same all round. It is bad for the men—the precious men, he said; but that it was probably bad for the women was not mentioned.

Similarly, in regard to technical education for the professions, the biological counsel must be the same—that we should seek to make the most of the complementary qualities. One of the keenest of intellectual combatants has said that, apart from maternity, the woman of strong physique or strong intellect may excel in any pursuit whatever her average male compeer. But even if this be true, we submit that it profits national efficiency more when gifted women do what no man could do so well, or when men and women work together as naturally as they once played together. We repeat what we said in *The Evolution of Sex* (1889): "The fullest ideal of the woman-worker is she who works not merely or mainly for men as the help and instrument of their purpose, but who works with men as the instrument yet material of her purpose."

Let us state one concrete case. It is certainly desirable that medical schools and medical posts should be open to women of special aptitude. There must be free experiment if social efficiency is

to be attained. But from our general biological point of view it seems that a more promising line of experiment would be that of providing specialised education for medical women—not "easier" nor "lower", or any nonsense of that sort, but *different*—so that there might arise, not duplication of one type of medical servant in the State, but two distinct types of medical servant.

It is an ordinary rule of all our lives that we try to find out the kind of work which is natural to us, which we can do most effectively or least ineffectively. We know that it is foolish waste to be always trying to do something which other people can do much better. We seek to make the most of our particular capacities, keeping economy of energy as well as efficiency in view. And our main thesis is just this same simple one applied to Man and Woman, that the most hopeful line of evolutionary experiment is that which seeks to make the most of the deep organic differences which were rooted long ago in the lowest beginnings of life.

WOMAN, AND HER SOCIAL EVOLUTION

After our discussions of Sex and its biological significance, and our later outlines of woman's characteristic features and her anthropo-social contributions, what remains to be said of her—woman herself, as we see and observe her (she has always known how to make us do that!), even to this day? Artists have ever painted and sculptured her, as from "the Venus of Les Eyzies" to the Venus of Milo in the Louvre; and these through widest contrast, from the Hottentot ideal of perfection to the Hellenic. Theologians and moralists have by turns cursed her and sainted her, fled her and worshipped her, and even philosophers have done the like as well. Psychologists, throughout the past generation especially, have laboured often and long to analyse her perplexing mentality, till now Freud and his resultant schools are busiest; and certainly with significant progress, and increasing demonstrations of her influences on man's life and throughout human society; and these often deeper and intenser than she had desired or dreamed. We present writers should be the last to undervalue the significance of sex, since with this our collaboration and its continued studies began full forty years ago; yet after all sex is for life and humanity, not these centred too exclusively on sex alone; deeply influential towards the flowering or the rotting of human life although it so deeply is. In our great modern towns, that have too often never been true cities, or no longer deserve the name, youth answers to *The Call of the City Streets* (by Jane Addams, of Hull House, Chicago; one of the most important social utterances of our time on the sex question in its social aspect). So sex often runs wild, and worse; while in later

life the sex-evils too often correspond to the old "possession by devils". All ordinary means, alike medical and moral, have been tried to cast these out; though as yet disease germs are yielding easily in comparison. Yet not only hysterics, but some lunatics, and even many criminals, are more understood; and all these often helped towards normal life. Yet what other advance among the sciences takes such intricate unravelling as for these? Not even the relativity theory or radiology, for choice among the hardest. Yet these devils, each and all in Protean dance upon and in their bearers' souls, are at length becoming known to the medical psychologist: and though always he gets his patient late, and often too late, it is no small triumph of science to be getting thus forward in diagnosis, and even in treatment; often finding alleviations and mitigations, even effective cures, up to mental and moral sanity and neural health.

As naturalistic inquirers into the range of normal sex, and this at its best and brightest, as from flowers and birds to human lovers and their poets, we have happily had to do with little more than the ordinary knowledge of its evils; yet enough to defend their courageous investigators from that too frequent criticism which would merely shirk facing the facts of diseased and morbid psychology. For from our first studies of sex, or sooner, we have felt how deeply true, despite touch of exaggeration, is the poet's intuition, long before the physician's diagnosis, that

All thoughts, all passions, all delights,
  Whatever thrills this mortal frame,
All are but messengers of Love,
  And feed his sacred flame!

Return, however, now to our initial problem—that of finding at least some clue to a fuller and better harmonised understanding of woman in life. And why not conversely?—thus primarily at her best, though at times for worse as well. After many years failing to find such mode of presentment, necessarily at once biological and psychological, and reaching throughout the range of woman's normal life and experience, a clue appeared where least expected, indeed least sought by scientific workers, though ever a joy to poets, and source of inspiration too—in Greek Mythology. How so? For all the arts, the world has long recognised that Greek inspiration was initiative, creative, masterly, often indeed supreme; and so for Greek literature, also in its ways supreme; and with the "Nine Muses" as forms of expression, to which none since have added a tenth. And so again for the sciences, in which indeed we have often got beyond them, yet largely by climbing from their shoulders. Yet their mythology? —they themselves ceased to take that seriously. And though our mythologists, in still comparatively recent times, have been dis-

covering this to reward serious study, their differences are still far too great to afford us any consistent theory of this mythic world; indeed they rather demonstrate it as a rich and varied mass of tradition, gathered from too many sources, and too many and varied minds to be reduced to system at all.

If so, so be it; yet this has never prevented any scholar from searching out this or that particular mythic creation, and so finding more in it than had previously been made clear. And though the next inquirer finds something else, why not? The poetic and symbolic imagination is not restrained to the single and unified presentments we seek in science: and as we humans throughout our course of life have very different aspects, relations, and developments of character, for better and worse, why not also the Olympian Gods, whom man created to surpass his own best? What bright vision then to share theirs; and so be each again, as with modern poet, like sculptor of old,

as one that sees
The very Gods arising 'mid their graven images!

THE GODDESSES AS TYPES OF WOMANHOOD.—That man, in his undying idealisation of woman, created the Goddesses in her image is surely plain; so who were they? What images of her had he to choose? In simplest answer, without going too far into their various attributes and perfections, we cannot but find among them, and indeed most obviously of all, the essential phases of woman's life. So let us consider them here in that order of age, as they passed before the minds of their poets and sculptors and those they worked for, each with his own loving and understanding concentration of choice. First then, as youngest, Hebe: and who is she, if not the child in her first beauty, her first helpfulness as well, eagerly waiting at table, filling the cup of Zeus? Then Artemis—Diana the huntress? Primarily the growing girl, still in maidenly unconsciousness of sex, and so running free and wild in Nature, of which she is still a part; so that even the later matured and "many-breasted mother" of the Ephesian temple remains type of Nature still, untouched by man. Next Aphrodite? Here is full-ripening maidenhood, rising from Nature's sea and awakening suddenly to her compelling charm, henceforth potent beyond those of all other goddesses; and hence winning the apple of Paris—the choice of youth—from her sublime and her enthroned successors. Of these, first and central to all, Pallas Athena, supreme expression to this day of woman's intuition at its brightest, its keenest too. See her terrible lance—no mere amazonian weapon, but also that "last word" which leaves man silenced, and even turned to stone, by her Gorgon shield of scorn. Thus too she is swift inspirer in battle, and thus gainer of victory for whom she favours. Yet gently

inspired too; hence honoured as giver of great arts of peace, from weaving the web to growing the olive.

But woman normally mates; whence the lovely Hera, the full-bosomed Juno, magnificent upon her peacock throne, in full attainment of her queendom. In time she matures, and to the matron, Demeter or Ceres, watchful of the cornfields and dispenser of their bread; and one day she loses her beloved daughter, as mothers must ever do; and often, like her, to some suitor not easily approved or come to terms with. Later, indeed last, woman sits as type of venerable age, richest of all in memories, keenest also in discernment of characters, events and their latencies, a veritable Sibyl. Sibyls, it must be confessed, were not in the Greek Olympus; nor were they usually old; but since Michelangelo put them in heaven, and humanity has ever honoured matriarchal old age (and above all since myths also grow and develop!), we may thus complete these Seven Ages of Woman.

MAN AS OLYMPIAN.—Place now these phases of woman's life upon the curve for man, conveniently opposite this. Who here first appears? Obviously Eros (Cupid), whom woman so deeply desires and rejoices in. And next? Hermes (Mercury), in his bright boyhood. Then the adolescent, Dionysos, rejoicing in his new strength, and thrilling towards woman, wine, and song. Then comes manly perfection and expression, Apollo with his lyre, facing Pallas herself. The struggle for existence has next its expressive type, so Ares (Mars) with lance or sword. Next comes elder maturity, as Hephestos (Vulcan), standing by his anvil as master of craft and skill, yet growing worn, even lamed thereby. Finally, in patriarchal seat, of authority and influence, sits Father Zeus, Jupiter Olympus. Here, then, are the "Seven Ages of Man", in their idealisation to divine images. From these Shakespeare's seven ages are the fallen analogues; though these we have ever seen more of, since ideals themselves fell away.

These old Hellenic presentments of the phases of life, and at their highest, thus need recalling; for may they not increasingly reward retaining, even renewing? So the evolutionary garden of our college cannot be wholly given to geologist and naturalist, to botanist and florist. It plainly also needs its cavern for introduction and recapitulation of primitive life; and with this, the ancient olive-tree of Pallas, duly honoured, even with temple in first outline. Farther on, the full Olympian circle, with seven pedestals on either side, for the ideal types of each sex in its life-phases. Within and around these needs space for meditation—and even for dance—each in its due time.

The contrasts so manifest in human life with its rises and falls still lack explanation: but the life-cycle of each sex offers indication of

this. Take Woman's. Here, with all due manly respect, we may be reluctantly compelled, by observation in life, to admit that as a matter of fact she does not always fully occupy the pedestal of Pallas; and even that such attainment seems at present comparatively rare. But Aphrodite's life-urge, with its doves and Cupids, chariots her, swiftly as may be, towards the realisation of her sex; and for this there are two ways, one within the Olympian circle, the other without. What are these in plainer terms? Though normally this life-passage is to wife and to mother, it may also "fall", even to courtesan and prostitute. But not every woman, in our Western world especially, either way effectuates her sex; so she may thus pass from girlhood-phase of Artemis to the grey hairs of Demeter. Here again her way divides—at best to sisterhood and to true motherliness; and this through sublimations, psychic compensations, and consolations—of which the old religious orders and the modern professions of social service alike offer such noble instances. Yet our own civilisation, through too many recent generations, has afforded too little of such outlets, and so left too many a "maiden withering on the stalk"; whence the term "old maid", with its harsh as well as pitying judgments.

Again, even the child Hebe may be shortened of her free growth to Artemis; with her helpfulness too constrained to labour, and this even to latest age. Again, on one side this has its psychic compensations, with simple yet worthy career; witness the "lay-sister" of old communities, or the faithful old servant, appreciated increasingly to her very end and bequeathing vital influence to honoured memory, like many an old nurse, as from Ulysses' days to Stevenson's. Yet alas, our social pressure too often reduces her to drudge and "slavey", and later even to slut; at times even to harridan, hag, and thence to crone.

Yet all those secondary and shortened life-phases may catch gleams from Athena's eyes; even those outside the normal curve of life: witness the often illustrious hetaira, the sharp-witted old maid, and the long-dreaded witch. Leaving psychology, may not the biologist here find a suggestive clue towards abating his perplexities over the many "abbreviations," which occur in the course of his observations of the phases and stages of development?

MAN AND HIS LIFE PHASES.—Turning to Man, the phases of his life-cycle exhibit corresponding abbreviations, with light upon many of his characteristic secondary types accordingly. So of these also a brief outline, since again suggestive for the better understanding of human life—and perhaps even also towards interpretations in biology.

To woman's eyes, man does not always attain to the perfect Apollo, even though he may think he does. But how much more

readily may Dionysiac youth rush onward and into passion to its utmost? In Greek Mythology we see the concentration of noble passion to worthy effort and highest achievements in Hercules, with his twelve labours; but for our matter-of-fact times, of the self-supposedly more "practical man", such myths are done with and forgotten. So our young Dionysos, left uninspired to Herculean aims, remains too much left directionless; and so may fall, through Bacchic joys, even to be a Silenus; or again to become seducer, "fast man", and worse; while Ares may waste his manly strength in brute force, as hooligan.

Man's life may again abbreviate its phasal course: so an old myth shows a brightly mercurial and Hermes-like youth, striking and seizing fire from Nature, and bearing it even to Vulcan's forge, as to Demeter's hearth. But Prometheus is left to poets, like poor Shelley; save that we still seldom fail to inflict like penalties on each fresh fire-bringer, whether of invention or of thought.

The Greeks knew well the Cypress-tree, with its small beginnings of leaves, perpetually young, and so growing on indefinitely—whence indeed our graveyard Cypresses, though now misunderstood as symbols of mourning instead of comfort. Thus their tales of the immortal Zeus showed Eros often beside him; and whoever can worthily prolong his years beyond the ordinary span has surely something of this secret, at once so obviously psychic, yet so deeply organic, of retaining childhood at its best throughout his thus long-growing life.

Are these Hellenic divinities then but casual mythologic dreams, of mere literary interest, or at best of sculptural appeal? So it has too long seemed; yet if they did not exist, would not the biological evolutionist, as he gained the courage of his opinions and the use of his imagination, have now to invent them?

By all means let researches continue into animal origins, and through sub-human links to lower human species, like those of which Piltdown, Neanderthal, etc., have yielded evidence; and thence again to our own species and its existing varieties, races, and mongrels. Yet is it not also time to be turning from this wellnigh exclusive preoccupation with the remote past, seeking to form some idea of man at his best, and thus of his possibilities in the future? And when we find both already expressed in this truly classic past, and beyond all our observant or evolutionary dreamings, do not such supreme presentments acquire fresh values and renewed significance?

How indeed can we explain our long-prevailing scientific apathy to these concrete evidences of human evolution, and towards perfection so far beyond our customary inquiries and studies? Mainly perhaps by the inevitable rebound from the would-be "classical education", which starved our scientific interests, and yet was too

much but verbalistic degeneration of classics proper. But as our studies of human origins and developments lead us on from prehistoric Europe, and thus through historic Hellas, must we not see with freshened eyes what our teachers at best too ignorantly worshipped, and realise anew the evolutionary significance of these supreme creations, of man into divine imagery?

For our ordinary biologic studies we seek normal types. In humanity we, of course, find these; yet types more or less subnormal are too frequent in contemporary civilisation: while beauty and perfection are now comparatively rare; in fact, do they not nowadays seem supernormal? Yet why not make experiment—as of setting a competent artist to draw for us, first the Olympian Sevens, and then good modern presentments of these phases of life in both sexes; and even in their modern costumes too? Will he not soon arrange, upon each curve of life, a series not a little recalling their Greek idealisations? And so too may we not stage these from our own range of acquaintance? We have indeed made a good many such experiments, and not without success—in fact beyond anticipation. The Greeks valued such types socially, while we appreciate them at best but individually. They used them as ideals, at once eugenic and eupsychic; so may not we do the like?

Here then we have the life-cycle of the sexes at their best clear before us. Next the leading abbreviations of its phases also, and these again towards advance or decline in development, for better or worse, and towards action good or evil. If so, we see our way more clearly, as towards disentangling the contrasts and paradoxes which have ever so perplexed the sexes, as to each other, and to themselves. For here we see no mere norms of development; the ups and downs we see in human life are sometimes toward supernorms, too often towards sub-norms; for where developments are not towards advance, but relaxed or arrested, there deteriorations, degenerations, or even perversions of various kinds, tend readily to come in. This clearing up of our conception,s of the phases and possibilities of human life, is significant for medicine, as indeed all the wise old family physicians so peculiarly know—and this for mind as well as body. The traditions of practical wisdom, elaborated in the past by its various forms of religious teaching and guidance, are also often being strikingly corroborated by the advance of psychological medicine; and they are even increasingly renewed and adapted to its curative endeavours. Yet neither the physician nor the priest is always fully accessible to such presentments as the above: so let us turn for a moment to more general readers. Older ones may remember, from some good few years back, Weininger's *Sex and Character*, and as of extraordinary vogue, not only in Austria and Germany, but in translations throughout the world. If they recall his essential thesis they will now see it plainly out-

lined above—as the two alternative courses of woman's realisation of her sex; although that author's pessimistic view and treatment laid especial stress upon the instinctive impulses and towards undesirable result.

Though Weininger may now be forgotten—as indeed on the whole is for the best—we cannot but recognise the creatively-poetic power and passion of Nietzsche, limited though may be our acceptance of all his teaching. Yet are not his fundamental concepts derived from his own tragic life-problems, even more deeply than from his Hellenic culture? Has he not thus truly prefigured himself first of all, with man's adolescence also, in his hard struggles, of passage through the stormy phase of Dionysos at his intensest, and towards his aspirations to attaining the serene perfection of Apollo? So, too, for his impassioned scorn and revolt against the contemporary world upon its lower sides, so much as above outlined. Above all, let us give credit to his aspirations at their fullest—not only as Apollonian, but at times Herculean, often to Promethean, and even to Immortal! As Zarathustra at his best, is not he much of all these, by turns and together?

THE EUGENIC IDEAL IN SCHOOL

The aim of eugenics—one of the oldest of ambitions—is the improvement of the racial qualities of future generations, and there is no nobler endeavour open to man. "Eugenics is the study of the agencies under social control that may improve or impair the racial qualities of future generations either physically or mentally." This quotation of Sir Francis Galton's familiar definition is sufficient answer to the ignorant or malicious suggestion that eugenics is altogether redolent of the stable and the barnyard. It might, indeed, smack of worse, but as a matter of fact it takes to do with character and intelligence as much as with physique. Its chief thought is of *racial quality*, the hereditary "nature"; but it is well aware that this cannot be expressed without the appropriate "nurture".

In this section we wish to discuss the extraordinarily difficult problem, how the eugenic ideal may be introduced into school education. Relatively little has hitherto been attempted in this direction, and it is doubtful whether we can wisely advance beyond giving hints for experiment and looking about for some general educational principles that have been shown to be sound in other cases, and that have some bearing on the present problem.

What is it then that we want? Certainly *not* to coerce youth into the acceptance of a dogma, but to stir the imagination into hero-worship. Certainly *not* to force something in from the outside, but

to develop what is normally there already—a feeling of kinship, an awareness that we stand and fall together, a pride of race. Certainly *not* to cloud the horizon with responsibilities prematurely anticipated, but to educate the conscience by the discharge of duties which, though real and not fictitious, are yet appropriate to youth.

To talk about *teaching* a pupil racial responsibility is to betray a detachment from realities. What we need to discover is the appropriate sunshine and rain and fresh air for certain buds which lie ready to be awakened to growth. We must seek for what physiologists call the liberating stimuli, and there are three whose efficacy is sure. First of all, there is:—

(*a*) The artistic stimulus, through poem and picture, through song and story, through the history of our race and the lives of its heroes. As one of our wisest educationists has said: "The power that may be exercised in the formation of character by the presentment of ideal types is as yet very imperfectly utilised." It is our problem to think out a strategy—of working towards a eugenic conscience, and to learn the tactics of artistic appeal. For the young mind, each in its own secret and unconscious recapitulation, is hereditarily open to the thrill of the undying voices of the past. It may seem a strange route to the Eugenic ideal, but is it not the surest that we know?

> Let statue, picture, park, and hall,
> Ballad, flag, and festival,
> The past restore, the day adorn,
> And make to-morrow a new morn.
> So shall the drudge in dusty frock
> Spy behind the city clock
> Retinues of airy kings,
> Skirts of angels, starry wings,
> His fathers shining in bright fables,
> His children fed at heavenly tables.
> 'Tis the privilege of Art
> Thus to play its cheerful part.

(*b*) The second stimulus is in *action*. Whatever you do, Stanley Hall says somewhere, don't lecture. One does not require to read *Stalky and Co.* to be sure of the futility of eugenic "jaws". For, as far as character is concerned, it is by living that we learn. And just as the play of animals is now recognised to be of vital importance as a rehearsal for the serious business of life, so there is much to be said for the proposition that the most effective citizens are often those who learned in their youth what it is to play the game. For that means self-expression tempered by loyalty, individual effort and yet subordination to the good of the whole, and besides that, the discipline of looking forward. The characteristics that may

develop, and do develop into racial responsibility are in the making in playing the game. Another line of doing by which youth may learn is suggested by such activities as scouting, especially when this is developed on broad lines, with a good deal of exploring thrown in, and with real enduring of hardness. It is difficult to conceive of anything more educative, as a change from the imperative and invaluable discipline of the schoolroom, than some active participation in the communal life, especially at some juncture when scouts are useful, though without any prematurely heavy burden of responsibility. Are there not many indications that our education requires to become more occupational and less bookish, more motor and less sedentary, more communal and less conventual? In any case, it will have to be admitted that one of the reasons why painstaking education is often disappointing is that the responsibilities are so largely fictitious, not real. The apprentice in a carpenter's shop knows what real responsibility is when he makes a wheelbarrow that won't wheel, or spoils a good tool; but the schoolboy "slacker" often gains no such valuable lesson. That he may be punished does not make him feel the responsibility any less fictitious. Our point is that *a discipline in real responsibilities* in youth is the natural condition of the desired development of the eugenic conscience.

(*c*) The third stimulus comes through the ordinary avenue of knowledge. But here again it is the indirect method that pays. Let a diagrammatic illustration suffice. It is easy nowadays to get an observation beehive, and a formicarium is also readily procurable. Now, it may be safely said that it is quite impossible for any normal pupil whatsoever—except a few who are born philosophers—not to be interested in the social life of the bees and the ants, especially if the teacher has added to an accurate knowledge of the facts just a dash of, say, Maeterlinck's art. But if this be true in regard to the insects' hive, can we believe that the study of a human society will prove less fascinating if we give it a fair chance? In spite of all our remarkable improvements, is it not too true still that we waste so much time over the Wars of the Roses that we seldom get near the beginning of an interpretation of the society in which we live? While there is truth in the epigram that activity is the only road to knowledge, it requires the supplement that accurate knowledge is the only sound basis for action in cases where you cannot trust your instincts. It is useless nowadays to expect a feeling of responsibility for future generations from pathetically unreflective "Johnnies" and tragically mis-educated "Jennies", who do not understand, who have never had a chance of understanding, what racial evolution means.

Racial evolution in school! Surely! For the idea that the present is the child of the past and the parent of the future is one of those

true and deep ideas which are also clear. It can be made real in a dozen ways, most convincingly from zoology and botany, from the bird-show and the flower-show for instance. And everywhere museums are springing up which are interpenetrated with the evolution idea, which show everything, from a word to a button-hole, from a Gloire de Dijon rose to a fantail-pigeon, as the long result of time.

It is to the naturalist's mind difficult to think of anything more useful in the education of the citizen than a well-thought-out, vividly interesting, yet not too easy, practical as well as didactic course of instruction, which should lead to a firm grasp of the general ideas of racial evolution and individual development, of the characteristic Darwinian idea of the web of life or the inter-relatedness of things at first sight far apart, and of the characteristic Pasteurian idea of the biological control of life. These ideas form a natural preparation for the eugenic ideal.

SEX-INSTRUCTION AND EUGENICS

Leaving the problem of the eugenic ideal, let us consider the question of definite *eugenic instruction*, including sex-instruction in schools. This is another extremely difficult question, another problem whose solution must be found by experiment. An attempt to state some of the pros and cons may be useful.

There is no doubt that many phenomena of modern life, especially in cities, are not eugenic, but kakogenic. Now, it is the opinion of many investigators who have paid special attention to the problems centred in sex, that instruction, or more definite instruction, would lessen "immorality", sexual vice, adolescence troubles, indecency, and pruriency. Ignoring the subject is said to be in part to blame for bad first impressions, discoloured views, morbid brooding, obsessions of fear, and some forms of sexual vice. All this handicaps eugenic progress.

For young children the best instruction is, theoretically, that given by the parents, especially by the mother. When this is given, it is well, especially if care is taken to avoid anticipating interest and to abstain from offering explanations which will be afterwards found to be untrue. We may tell a child to wait for an answer, but we must not give the child an untrue answer. Prof. Stanley Hall emphasises the advantage of getting the right presentation first, preoccupying the mind with a dignified wholesome view.

But we have to face the actual facts. Few parents give any sex-instruction at all. Few can do it well. Few, for instance, are able to utilise the indirect, impersonal, biological approach. Most parents are too shy. Moreover, the personal aspect of the case rises obtru-

sively in the boy's mind when his father speaks to him. In large sections of the community the boys and girls leave the home in early adolescence. The family is not the social unit it once was; and while we do not wish to acquiesce in this as a necessity, we have to admit it as a present fact. Furthermore, those children who most need guidance, because of inborn predisposition to go wrong, are the least likely to get help from their parents. It all comes to this, that in many cases, if not in most, information regarding the most important function in life is picked up haphazard, often in an inaccurate and discoloured form, often from sexually precocious or perverted acquaintances. Is it not quite clear that instruction by parents requires to be supplemented?

It will probably be admitted by all that every college should have its voluntary course of instruction in bodily and mental hygiene, in the art of life, in genetics and eugenics, and that every college should have its wisely chosen confidential physician who would save the nation untold wastage, who would save in the year the salary of his lifetime. In many cases, however, advice at college age comes late, not too late perhaps, but unfortunately late. Can nothing be done earlier?

Instruction in regard to the facts of sex has been tried in a considerable number of schools in America, Germany, Hungary, Switzerland, and Finland, and in a very few cases in Britain. It remains, however, in an experimental stage.

The instruction given deals with (1) the elementary physiology of sex and reproduction—how life is continued; (2) the significance and the dangers of adolescence; (3) hygienic aids to self-control and clean-mindedness, the ideal of physical fitness, and the racial significance of sex.

The instruction is sometimes given quite by itself, to which most educationists object, and sometimes linked on to nature-study and biology, human physiology, domestic science, home-making studies, hygiene, economics, and social problems.

The instruction is given by the headmaster or headmistress, or by the class teacher, or by the teacher of biology, physiology, etc., or by the school physician, or by means of books and pamphlets. But there is great diversity of opinion in regard to the best method.

But we must not hurry on too quickly. There is a previous question, whether there should be in school any school-instruction whatsoever bearing on sex and reproduction. Many wise people think that there should be none, and for the following reasons:

(*a*) It is pointed out that sex, which is the physical basis of one of the noblest and most personal expressions of the human spirit, is a very delicate matter. It is like religion; if you speak about it unwisely, you may do much more harm than good. To which it may be answered that if saying nothing were working well, we should

all wish to leave well alone. But it is not working well. Moreover, as the vocation of the teacher is increasingly recognised as one of the most honourable, we shall get teachers more able to undertake difficult tasks.

(*b*) It has been said that it is a terrible responsibility to break brutally on an adolescent's reserve of mind. But this is a question-begging objection, for there is no occasion for psychic violence, and there is no brutality in some good sound biology. There are many methods of indirect approach—some of the subtlest of which are beginning to be opened up by the suggestions of Freud. There is nothing brutal in the suggestion that there should be a carefully prepared chapter on the physiology of sex and reproduction inserted even in the school textbooks of physiology, some of which continue to be published on the grotesque assumption that man has no reproductive system.

(*c*) Doubt is also expressed whether the education authorities would be justified, even if willing, in attempting intrusion into what ought to be a parental responsibility. But the parents usually do nothing in the way of discharging this particular responsibility, and a parental revolution, because the school was trying to do what they ought to do themselves, might be as wholesome as it would be hypocritical. A wiser answer is probably that the mode of sex-instruction chosen should be one that is not too far ahead of contemporary public sentiment.

It is easy to argue oneself into a *laissez-faire* policy until one comes again face to face with the actual facts—of unwholesome ways of looking at things, of morbid curiosity, of bad habits, of filthy-mindedness, of thoughtless immorality, of disease, of habitual vice. These are ever dragging evolution in the mud, and the eugenic ideal of positive advance cannot hope to find wide realisation unless we try also to lessen the kakogenic handicaps.

It must be noted that unless we supply wholesome instruction, the mind of the youth tends to be discoloured by unwholesome information gathered surreptitiously.

It is probable that every large school includes a small percentage of abnormal pupils, who infect others with their own unfortunate perversions.

If nothing "straight" is ever said by anyone, it is difficult to deny the justice of the sufferer's reproach—which is not confined to Brieux's plays—"But you never told me anything about that".

It should be noted, too, that the sex-instincts in man are general rather than sharply defined. That is to say, we have, in regard to sex functions, very little instinctive knowledge of what various phenomena mean, or of what is normal, or of what is to be carefully avoided. A boy or a girl may slide into bad habits without being well aware of what is happening.

These are a few of the considerations which lead some who have given careful attention to the subject to think that there should be *some* sex-instruction in schools. And in working towards something practicable, it may be of service to point out that the instruction will need to be varied with reference to different sections of the community, and with reference to the differences between girls and boys.

Taking the first point, one does not, of course, imagine that the dangers and difficulties involved in sex are restricted to particular sections of the community. They are universal—we are all tarred with the same brush—but they alter with altered circumstances—from the one-roomed house to the unnatural detachment from home involved in the residential public school. The counsels given by the wise headmaster or the wise school physician would be very different in different cases. It must be remembered, too, that habits are formed in the concrete, by habitually doing or not doing something, and that if the school conditions have tended to the establishment of a vicious habit of word, or thought, or deed, there is not much hopefulness in the school discipline saying "*don't*". This leads one to make the obvious remark that the problems of sexual vice and the like cannot be dealt with, either theoretically or practically, by themselves. They are wrapped up with problems of housing, occupation, wages, interests, use of leisure hours, education, civics, and what not. Everyone knows the dismal power of the economic and occupational factor in keeping up the traffic in immorality.

What seems the practicable line of advance is to think out a graduated series of educational methods, leaving it to the discretion of the teacher to decide how far along the series it may be profitable to go.

(*a*) Much may be done in the nurture of adolescence by developing external preoccupations and interests and real responsibilities; by opening paths of legitimate excitement (in work and play for both boys and girls, in art and wholesome adventure, in dramatic and musical exercise); and by discipline in enduring hardness (e.g. in scouting, in boys' brigades, in girls' guildries, in climbing and swimming and exploring).

(*b*) The highest value is to be attached to all forms of education (religious, ethical, and imaginative) which fill the mind with noble examples, which exalt the conception of human love by associating it with the chivalrous, the poetic, and the romantic, and which set a premium on self-control, courtesy, mutual respect, and healthy-mindedness.

(*c*) While respecting the natural instinct of reserve in regard to sex questions, something might be done to suggest that the deep reason for mystery is because sex is sacred, not because it is

inherently shameful or unclean. From history and literature it is surely possible to suggest that control and chastity make marriages happy and nations strong, while the *corruptio optimi pessima* is already hell.

(*d*) Much may be done through Nature Study (for younger pupils) and Biological Studies (for senior pupils) to remove the facts of sex and reproduction from an entirely human and personal setting, to exhibit them as natural phenomena observable at many different grades of evolution, to put an end to pruriency, and to make the big facts concerning the continuance of life familiar in the botanical and zoological fields—leaving it to ordinary intelligence to see the human applications.

(*e*) Beyond that it may be possible to go, in the way of more definite sex-instruction in the senior classes in schools, for boys in particular. It is probable that the instruction will be most successful when it is linked on to, and arises naturally out of, studies in natural history, biology, physiology, domestic science, hygiene, social problems, and the like.

It seems quite plain that girls require much gentler sex-education than boys; and the difficulty cannot be ignored that, as things are at present, a large proportion of the girls will not marry. Thus it may be distinctly dangerous to bring to the focus of consciousness instincts which often remain normally at a subconscious level.

It seems also quite plain that when sex-instruction is given—whether by the headmaster, the headmistress, the science teacher, the school physician, or by lending booklets—caution must be exercised not to anticipate interest, not to excite, not to deal with the pathological, not to frighten, not to pretend that men and women are angels, and not to say too much!

CONCLUSIONS

Perhaps we have given too much prominence to the problem of sex-instruction, but that has been done deliberately in the conviction that the lack of sex-instruction is one of the great barriers to eugenic progress.

To return to the main theme of introducing the eugenic ideal in school education, three definite suggestions have been made. We may summon to our aid the witchery of art; we may begin an apprenticeship in services which make towards racial invigoration; and we may appeal to the intelligence by making the big biological ideas, e.g. of evolution, variation, heredity, selection, the web of life, and the biological control of life—vividly living concepts, or, in any case, seeds that will develop in the mind.

But is there not something more needed to win any great measure

of success? Is it not significant that Sir Francis Galton, who so clearly recognised that eugenics must pass from science into practice, was also strongly convinced that progress would be slow until the eugenic ideal came to have a religious value? When it begins to sway us through and through—this vision of a nation healthy alike in mind and body; when we come to care more about that than about anything else, then we shall overcome our difficulties and our timidities, our objections and our sloth. We shall know eugenics to be "a virile creed, full of hopefulness, and appealing to many of the noblest feelings of our nature". And, *having made sure of sound eugenic precepts*, we shall hearken to what was said to the ancient people of high eugenic practice and ideal—"and thou shalt teach them diligently unto thy children, and shalt talk of them when thou sittest in thine house, and when thou walkest by the way, and when thou liest down, and when thou risest up, and thou shalt bind them for a sign upon thine hand, and they shall be as frontlets between thine eyes; and thou shalt write them upon the posts of thy house and upon thy gates". The old instruction of the Book of Proverbs is well worth popularising anew, in these matters and others also.

CHAPTER V

BIOPSYCHOLOGICAL

ANIMAL BEHAVIOUR.—In the strict sense behaviour implies a chain of actions adjusted towards a particular result; thus a single reaction of an Amœba is hardly worthy of the name, whereas the pursuit of one Amœba by another must be so regarded. Behaviour is a purposive concatenation of diverse activities. A single reflex action, such as drawing our finger away from a hot coal, is hardly at the level of behaviour, being no more than one process, soon over and done with. Yet reflexes are often linked in a chain, and the physiological side of instinctive behaviour may be regarded as a long chain of linked reflexes. Thus it seems impossible to draw a dividing line, and in this chapter we are using the word behaviour in a wide sense.

If we were taking a survey of animal behaviour from the purely physiological side, we should naturally begin with relatively simple responses to stimuli, such as reflex actions, and from these we should work gradually upwards to activities which require psychological terms for their description.

But here it is useful to reverse the order of treatment and begin with the highest animals and their most striking doings. For we are passing in this chapter to the definitely psychological level; and while the mental or psychical factor is insistently clear among birds and mammals, it is often dim at lower levels, until among the simplest it is only hinted at; and the question rises whether it may not be usefully ignored. It should be noted, however, in regard to cases like tropisms, where the simple behaviour seems to be adequately describable in neuromuscular terms, it does not follow that the *origin* of the enregistered predispositions can be thus accounted for. Moreover, as we shall afterwards see, the psychic life of an animal is not restricted to the mental processes, such as image-forming and memory and sometimes inference, that lie immediately behind or form the subjective aspect of the behaviour. There is the often intense emotional activity of the creature and the tumult of desire. Even when an apsychic description can be given of an isolated chain of acts, this may be entirely inadequate for the life as a whole.

(I) RATIONAL CONDUCT.—In the more distinctively human activities of a man there is rational conduct, which cannot be described except in terms of *conceptual* inference. There is working with general ideas or concepts, such as those utilised in building a house; or there is a control of the main tenor of life in reference to

some clearly conceived purpose or ideal; or there is an expression of an abstract idea in significant artistic form. Whatever definition be used there is general demarcation of rational conduct, as distinguished from intelligent behaviour. So far as is known, this higher level is not definitely reached by any animal; though, as we shall see, there are adumbrations of reason in the higher apes.

(I*a*) SUBCONSCIOUS THINKING.—Those disciplined in prolonged and resolute thinking at a high level often acquire great expertness. Habituation in rational and abstract discourse is familiar to the mathematician and the philosopher; and there comes to be an enregistration of the habit of experimenting with general ideas in the mind. That this is possible depends in great part on the use of symbols, such as notations, graphs, visual images, and most familiarly, of course, words. That intellectual experiments may continue in dreams is well known; and there are many instances of effective unconscious cerebration, when the solution of a problem appears without deliberate effort. We attach importance to this, because there is reason to believe, as we shall see, that every level of activity has a tendency towards some measure of enregistration or automatisation.

(II) INTELLIGENT BEHAVIOUR.—The next level is that of intelligent behaviour, which cannot be adequately described apart from *perceptual* inference. There is evidence of some understanding of the situation, some perception of relations, some adjustment of old means to new ends, some degree of *judgment*. Much of man's activity is on the intelligent plane, and the same is true of many of the doings of the higher mammals, such as anthropoid apes, horses, dogs, and elephants. At lower levels among vertebrate animals it is more sporadic, being mingled with what is predominantly instinctive. Among Invertebrates it is rare, though it may occasionally intervene in the marvellous routine of instinct. We are, of course, using the term "instinct" in a precise way, to denote an inborn or hereditary capacity for doing apparently clever things without any need for apprenticeship; and the student will understand that some of the instinctive achievements of ants and bees are at a much higher level of intricacy and effectiveness than a simple intelligent action on the part of a mammal. But they are on a different line of evolution.

INTELLIGENCE OF APES.—At this point some account must be given of the recent studies on the behaviour of the higher apes—studies which differ from most of the older ones in three ways: that expert psychologists, accustomed to detect the pitfalls of interpretation, have taken a leading part in the inquiry; that care has been taken to supplement observation with experiment; and

that the animals have been studied in conditions of comfort and along with their fellows. Thus Köhler, primarily a psychologist, made his observations and experiments in Teneriffe, where the climate suits the chimpanzee, and under conditions where the animals lived together cheerfully. As that observer remarked, a solitary chimpanzee is no longer a chimpanzee. What Köhler has done is to show that chimpanzees often solve problems in an intelligent way, appreciating the significance and relatedness of different links in a chain of acts, and apparently making perceptual inferences in reference to visible situations. Thus they would put one box on the top of another, even making four-storied erections, in order to reach a banana suspended from the roof. They learned to join two pieces of bamboo rod together in order to make a length sufficient to reach a prize outside their cage. One of them bit at the end of a piece of stick, reducing the end till it was of a size suitable for insertion into a bamboo rod that had to be lengthened to reach a desired object. There are many such examples, well documented and well criticised. It is true that chimpanzees must have the factors for the solution of the problem within their visual range, for they seem to have a very limited capacity of working with mental images; but the outstanding fact is that they are far more intelligent than was suspected.

Noteworthy is Dr. Hornaday's account of an orang that discovered the effectiveness of a lever, and then proceeded to find other levers of various sizes, including the heavy trapeze-bar with which it was possible to prize asunder the vertical bars of the cage, thus allowing the orang to gratify his long-cherished desire of looking round the corner at his neighbour in the next cage.

Köhler records some interesting facts in regard to the ape's appreciation of a mirror. He gave a hand-mirror to one of the female chimpanzees, and it at once became a source of delight. It was passed from one to another, and the reflection was evidently recognised as that of a chimpanzee. But in every case and in diverse ways the chimpanzees made attempts, while holding the mirror in one hand, to catch the other chimpanzee "behind the looking-glass". Very rapid surprise movements were made over and over again, and the futility of the attempt did not suffice to dislodge the fixed idea. Even more interesting, however, as indicative of an active brain, was that the chimpanzees proceeded to discover new mirrors for themselves, pieces of polished tin and the like, into which they would gaze intently. A striking situation which Köhler pictures is that of chimpanzees gazing abstractedly at their reflection in a rain-puddle! May this not have been reflection in another sense—even the dawn of self-consciousness!

Prof. R. M. Yerkes, well known for his careful study of the "dancing mouse", made an intimate study of two young chimpan-

zees, one of which was in vigorous health. As an expert psychologist he was peculiarly careful not to rely on single observations. Compared with the critical scrupulousness of Köhler and Yerkes, most of the old work—though not that of Romanes—appears relatively anecdotal.

From Yerkes's results it is plain that there are very marked individual differences, and that bodily health counts for much. The male, Chim, who was in vigorous health, showed himself sanguine, venturesome, trustful, friendly, and energetic. The female, Panzee, who was in poor health, showed herself distrustful, retiring, and lethargic. Chim's behaviour suggested in most cases unusual intelligence; Panzee's, on the other hand, suggested stupidity. This points to the importance of the health factor. Sometimes the difference in behaviour might have to do with sex. Thus the male habitually strove to evade the disciplinarian, while the female tried to get into his arms. One day Chim carefully plucked some blossoms and presented them to a lady attendant. He would dance in a lively way, keeping time to music; but Panzee, though interested in music, never danced. Chim constructed nests, but though Panzee once or twice climbed the tree to take a look at one, she was not much interested, nor did she herself show any building bent.

There was abundant evidence of high sensory equipment, visual in particular. But again it was the vigorous Chim who was most interested—even in the distant mountains! He also was much quicker to appreciate something of the significance of a new situation. Thus it was striking to see Chim dealing with a juicy orange halved across the equator, for after a little experimentation he learned to extract the pulp without losing a drop of the juice. Panzee's technique in eating a half-orange was crude and careless in comparison, and commonly resulted in the loss of more or less of the juice.

Of intelligent appreciation of a problem perhaps the best example was in connection with lifting one box on to another in order to secure a banana which was otherwise out of reach. The solution came within five minutes. Dr. Yerkes has no doubt that Chim worked with ideas and made inferences. "Most surprising and impressive in Chim's behaviour", he writes, "was the continuity of attention, high degree of concentration on his task, evident purposefulness of many, if not most, of his acts, his systematic survey of problematic situations, his rapid elimination of unsuccessful acts or methods, and his occasional pauses for reflection."

In this connection we may here recall Darwin's story of the monkey-trainer who used to buy his animals from the dealer for £1 each, but offered up to £5 each if he might have leave to choose, one by one, out of batches to be lent him for a period of trial. When Darwin asked him the reason for this, he explained that the only

monkeys he could really train were those who could pay attention; and that these were not by any means common. Here there is a point at once of interest and of practical difficulty for experimenters, and one suggestive towards evolutionary interpretation as well.

Mrs. Learned made a careful record in musical notation of all the sounds habitually uttered by the two chimpanzees already mentioned. They fall into four groups, according as they were made while waiting for food, while eating, when in company with persons, or when two chimpanzees were together. Seventeen of the sounds begin with gutturals, like *gho* in greeting friends; four begin with an aspirate, like *ho-oh* in alarm; five begin with nasals and labials, like *ngak*—a food-word; five begin with vowels, like *ah-oh-ah*—a half-scream of apprehension. There is a much larger repertory of vocalisations than was suspected; and these might form the basis of a language if the chimpanzees began to imitate sounds persistently, as parrots do. But there is almost no trace of this. So Mrs. Learned concludes: "Although the young chimpanzee uses significant sounds in considerable number and variety, it does not, in the ordinary and proper meaning of the term, speak."

As words seem to have played a very important part in the evolution of human intelligence, we make no apology for lingering over the question: Have chimpanzees a language? What is said here will apply to other gifted animals like dogs. In the first place chimpanzees have the same vocal instruments as man has; there is a close resemblance in the larynx and in the vocal cords. In the second place they have "a good voice" and a considerable gamut of sounds, which are used consistently, e.g. as expressions of joy or of anger, or in particular situations, such as the announcement of dinner.

But the chimpanzee has not been known to *imitate* a new sound as parrots do; and this, along with some expression of a judgment, seems to be the essence of language. Parrots have made the first step, for many are quick to pick up a new sound; but even the cleverest parrot is not known to make a sentence expressive of its own judgment. That it may repeat a sentence, often jerking it out with uncanny appropriateness, is well known, and may sometimes illustrate "association learning"; but the parrot's sentences are simply, so to speak, very long, much broken up words.

Various attempts have been made to teach chimpanzees to speak, but without success; though it is very interesting that Yerkes's Chim occasionally mumbled a little when people were talking in his presence, that he became interested in listening, and that he sometimes answered back in an appropriate way to certain noteworthy sounds. One of the methods of instruction was to arrange for the mechanical delivery of pieces of banana on the table of Chim's observation-room, and to utter the sound "ba, ba!" as a signal for

the appearance of the fruit. For about a fortnight this kind of lesson was given once or twice a day, and Chim was much interested and very appreciative. The hope was that the ape would learn to say "ba, ba!"; but it never did. Another method was to hang in the cage an apparatus loaded with pieces of banana, which were delivered to the chimpanzee in succession whenever the experimenter said "co, co!" But Chim did not get beyond "certain slight and unconvincing imitations of attempts to make sounds when facing the apparatus."

Another educational apparatus consisted of a board on which was a small box hinged on one side and provided with a spring, which when released would raise the box and disclose a banana. As the box had a wire-mesh cover, this method had the advantage that the pupil could see the fruit. Prof. Yerkes took the contraption into Chim's cage, secured his attention, and made the sound "na, na!" distinctly and emphatically a few times, thereupon releasing the spring and disclosing the prize. Sometimes he would begin to eat the banana to intensify the ape's interest. This was done over and over again, but the chimpanzee never learned to say "na, na!" The only kind of lesson in this direction that had any positive result was that the ape learned, as a dog will learn, to utter a particular sound *of its own* when it wanted to get food.

Chimpanzees are so intelligent and sympathetic that we cannot accept the philosopher's remark that animals would speak if they had anything to say. What, then, is the reason for their relative reticence, for their not advancing from words to language? Is there any answer but that the ape-brain has not reached the degree of differentiation that made a speech-centre (and its correlated psychobiosis and biopsychosis) possible? The anatomical facts point to a consistent variational trend of neo-pallial complexifying, from the marmoset level to man's; and there is no special problem in the fact that the apes' brains have not reached the intricacy that makes language possible.

To appreciate the psychological significance of these and similar achievements, let us contrast them with others. No one who has studied the terms would propose to find in the apes' behaviour any evidence of Reason, as distinguished from intelligence. For Reason is taken to imply *conceptual*, as distinguished from perceptual, inference. Reasoning may be effected at an intelligent level, but Reason implies experimenting with general ideas or concepts. So far as we know, there is no carefully recorded instance of animal behaviour that demands for its adequate description that we should credit the creature with general ideas and a capacity for working or playing with them. Man is often intelligent and occasionally rational; animals are often reflex and instinctive, and occasionally intelligent.

Köhler remarks that while the chimpanzees made some clever hits, they often failed to take a step which a child would have thought of. Picture, for instance, the chimpanzee who followed others (not a very common procedure) in making a four-story erection of boxes in order to reach the hanging fruit. Unluckily she placed the fourth box with its open end up, so that when she climbed into it, she was little nearer the desired banana than if there had been only three boxes. Not understanding the relations of things, and only dimly appreciative of a concrete "If this, then that", she was nonplussed. Unable to correct her mistake, or fatigued by unwonted mental exertion, she curled up in the topmost box and fell asleep.

When we ask why an animal with a fine brain is not cleverer, we should recall the biological commonplace that no creature is likely

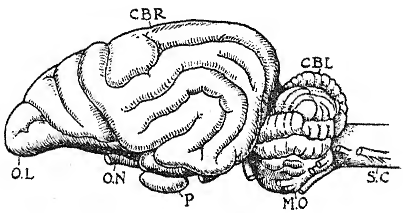


FIG. 90.

Side View of the Brain of a Dog, showing the convoluted cerebral hemispheres (CBR), the transversely grooved cerebellum (CBL), the medulla oblongata (MO), the pituitary body (P), the crossing of the optic nerves (ON), the olfactory lobe (OL), and the spinal cord (SC). Through the predominant development of the cerebrum there is a covering over of the optic thalami region and the optic lobes. Similarly the cerebellum conceals the medulla oblongata.

to show much more cleverness than the conditions of its life demand. The anthropoid apes are strong and secure; they are as intelligent as is required, just as is the case with a Golden Eagle. Till the higher values are more than adumbrated, increase of knowledge would be too apt to mean increase of sorrow. It would not be good for an animal to have much imagination unless, indeed, it is going to begin a new ascent of man.

But after we have granted that apes are as intelligent as they need to be, and that their brain is neither as large nor as finely differentiated and integrated as ours, the question rises: What are their particular handicaps? The answer is twofold: (*a*) that they seem to have a relatively poor repertory of mental images, and (*b*) that they have no language. The first drawback is illustrated by the general result of experimentation that the apes are seldom able to solve a new problem unless the elements in the solution are within its visual range at the time. A child might have a mental presen-

tation of what would fill the gap, and might search for it in a widened environment. Not that any hard-and-fast line can be drawn; for there is the well-known case of Miss Cunningham's young gorilla, who, after sulking a little on being refused a seat on her lap, searched round the room for a newspaper, which he proceeded to spread as an apron over his teacher's dress.

The second handicap is the merely incipient character of ape language. Chimpanzees have many words indicative of particular experiences, such as meals and danger, or of particular emotions, such as joy and resentment; but there is no expression of a judgment in even the tiniest sentence, and there is not, as is seen in parrots, any social imitation of particular sounds. But it is language that widens the folding-doors of the mind that necessity and visualisation have opened.

INSTANCES OF INTELLIGENCE.—It is all very well to say that we mean by intelligent behaviour a chain of actions which cannot be adequately described without crediting the animal with some degree of perceptual inference; but it is necessary to adduce definite cases that illustrate the contrast between this and instinct.

We begin with a previously unpublished case, which we owe to a careful observer, Arthur H. Sim. A cock homer pigeon was due to relieve the brooding hen, who was sitting in a dovecot. This had an alighting-board at the entrance, and the door itself was a sliding shutter working in a bevelled rail. As the entrance was half-closed, the cock pigeon got his head and shoulders in, and succeeded in shoving the shutter along. But the observer frustrated his successful entry and put him outside again, adjusting the shutter in the original position. Whereupon the pigeon repeated the effort with success, and this was done several times in the course of a few minutes, the bird becoming increasingly expert.

After a short time the experiment was varied, and a small piece of wood about two inches long and half an inch broad was laid in the bevelled rail in such a way that the door could not be pushed along far enough to let the pigeon in. After some fruitless pushing, the pigeon seized the piece of wood in his beak and threw it on the ground. He then slid the door along and entered the dovecot.

But he was not allowed to settle down, and the performance was repeated several times in the course of a few minutes. As the bird was always baulked of his reward, he gave up trying, and remained passive on the alighting-board for almost ten minutes, the observer standing three or four yards away.

The next step was of much interest. The observer went into his house close by and watched from a window. As soon as he had reached his post of observation he saw the pigeon seize the piece of wood and toss it into the air, afterwards effecting entrance as he

had done before. The observer removed the pigeon again and retired to the house, where he saw precisely the same performance. In fact, the experiment was repeated several times, always with the same result. When the observer remained standing near the dovecot, the pigeon did nothing; when he went into the house, the pigeon immediately lifted the jamming piece of wood and slid the door along. After the observations had lasted for about three-quarters of an hour they were discontinued, partly because nothing new had happened, and partly because the cock pigeon became exceedingly impatient to take up his position on the nest. We have given the case in detail, because it is a good illustration of the kind of behaviour that must be called intelligent, though the prompting of the whole was instinctive. There are four points to be noticed: (*a*) the dexterous sliding of the door along; (*b*) the removal of the piece of wood that prevented the door being opened far enough; (*c*) the cessation of endeavour when the pigeon perceived that his solution of the problem did not meet with its due reward; and (*d*) the immediate repetition of the activity when there seemed to be a chance of success.

UNUSUAL HINTS OF INTELLIGENCE.—Part of the schoolboy lore of long ago was that if you took one egg out of a clutch the parent bird "would not notice", but if you took two it would desert. This belief in a power of appreciating numbers has been held by naturalists wiser than schoolboys; and cases are on record of both birds and mammals that behaved as if they missed a member of their flock or family who had been secretly removed. But when a parent leads about its young ones for a considerable time it has probably an awareness of each little individuality, and might be perturbed by its absence without being able to verify this by counting. It is certainly not by counting heads that the bees of a hive became quickly aware of the fact that the queen has been removed.

It is held by some sportsmen that rooks and the like are not deceived when all the intruding eliminators walk away save one, who remains in concealment. Yet it may be that the rook does not say to itself, "Six came and five have gone, therefore one remains." Fine-brained bird it certainly is, but one must first make sure that it did not notice the sportsman's concealment. Romanes reported long ago an interesting case where two crows on their nest were not deceived when three men threatened them and two went away, while the third slipped quickly into a shed. Nor were they deceived when four came and three went. But when five came and four went, the crows did not notice and came down from their nest. The inference was that the crows could not count beyond four, yet it may have been that the rapid act of concealment was more difficult to detect as the numbers increased.

Unforgettable are the lessons in arithmetic given by Romanes to the chimpanzee Sally in the Zoo. In the course of time, when the teacher asked for three straws, Sally gathered one-two-three. First holding them in her mouth, and then taking them in her hand, she presented them between the bars of the cage. And so with four and five straws, but not successfully with more. An association seemed to be formed between the sound of the number asked for and the number that should be gathered, and to this extent Romanes believed that Sally could "count". He was inclined to go farther, for he told us once that when Sally was in a hurry to get her reward she had been known to bend a straw so that its two ends stuck out between her finger and thumb. She saved time by making one straw count double, and when the reward was refused she would straighten out the bent straw and pick up another to complete in the fit and proper way the number asked for. If this case were well established it is very important; but Prof. Hempelmann, in his *Tierpsychologie*, points out that great care is necessary to exclude the possibility that the very alert ape is not taking advantage of conscious or unconscious signs of approval on the part of the instructor or the gallery. If the clever creature, having gathered three straws, sees that the audience is satisfied, then it gathers no more. Prof. Köhler's observations on his happy chimpanzees at Teneriffe yielded no evidence of any ability to estimate numbers; and Lord Avebury's clever dog, Van, after three months of lessons, had made no progress towards a practical appreciation of the number of strokes on white cards. This dog, it may be recalled, was able to go to a box of cards and select the three whose letters spelt T-E-A, or O-U-T, or the like, but when it was asked for a card with a certain number of strokes, its answers, even after long tuition, were quite at random. That is to say, the dog had either failed to establish any association between the sounds one, two, three, or four, and the images of one, two, three, or four black strokes, or else, less probably, it had failed to detect any difference between the cards bearing different numbers of strokes.

An old and simple experiment with horses hints at some appreciation of quantity, if not of number. The horse was offered on a table a choice between one lump of sugar and two or three lumps. It always preferred the number greater than one, and yet it showed no preference for three over two. This is a better kind of experiment than that of the black strokes, for lumps of sugar are of direct practical interest. Perhaps, as we have said, the preference was based on a volumetric rather than on a numerical estimate. Of course, the sides at which the sweet alternatives were placed were continually changed.

In a striking experiment by Katz and Revesz; grains of wheat were arranged in a row, fixed and free alternately. Very quickly the

hens learned to try only every second grain. Then the loose ones were separated by two fixed ones, and the hens soon saw through this. But when the loose grains were separated by three glued grains, the hens gave it up. Yet they learned to take two loose ones in succession, separated by a single fixed one. This did not mean that the hens could count up to two, but not up to three; it rather meant that they could, so to speak, register a group of two as a unity, but not a group of three! What seems to have been proved was the hen's quickness in learning to suppress useless peckings; but the experiments should be repeated. One would like to know from those who have driven cars about the country for some years whether there is any marked suppression of useless movements on the part of the farmyard hens that straggle on to the roads.

Some of Revesz's hens had very strong views on the greater profitableness of a ten-grain heap as compared with a six-grain heap, and did not hesitate in preferring 3 to 2, 4 to 3, 5 to 4, and 6 to 5. But this was probably due to volumetric, not numerical, impressionism. And so when a brooding bird is uneasy over the theft of three eggs out of six, the probability is that its perception is not much more than a vague awareness that the picture has been disturbed.

We shall not go back to the "thinking horses" of Elberfeld, which could extract cube-roots, stamping out the answer with their feet; and we do not hold with the enthusiasts who believe that ants and bees notice the fluctuations in their numbers as such, altering their behaviour accordingly. In fact, we think there is little evidence at present that animals can count more than a very little. For counting requires counters, either words or symbols or tallies, and to find more than the beginnings of these among animals requires a generosity to which we cannot rise.

Utilisation of the Fortuitous.—Before a chimpanzee hit upon the device of piling one box on the top of another to reach the high-hung fruit, it tried other methods, such as climbing, swinging violently on the hanging rope, and standing on the shoulders of another ape. As these all failed, it was driven to further experimentation. But all that was done was on the line of purposeful and deliberate experiment towards an end in view. Yet there are other cases where the intelligent factor operates by taking advantage of a fortuitous occurrence, and we need not depreciate this too much, since many of man's inventions have been made in a more or less similar way. It is said that the Greek eagle lifts the Greek tortoise in its talons to a great height, and then lets it fall on the rocks below, with the result that the extremely strong carapace is broken and the muscles exposed. This is an ingenious way of utilising an almost invulnerable animal, but it may have been discovered quite fortuitously. Eagles often lift booty in their talons without stopping in their wild rush, but they often let their captive fall. This would be

very apt to occur with a smooth-backed tortoise; and the intelligence might lie in taking advantage of a useful accident and one that would be likely to happen over and over again and with different eagles. Similar behaviour has been often observed on the part of herring-gulls, which lift crabs, sea-urchins, and clams in their bills and let them fall on the rocks or shingle below, with the result that the hard shells are broken. In some places and on some occasions this may be observed frequently among the gulls, and then it may not be observed again for a long time. This requires further observation; but it suggests repeated re-discovery as the result of a natural accident. Rooks deal in a similar way with freshwater mussels.

Caution Necessary in Experiment.—As a general rule it may be said that animals are not cleverer than they need to be; and mistaken inferences are sometimes drawn from cases where the animal shows little or no hint of intelligence, simply because the situation made no appeal to its interest or desire. This is well illustrated by domesticated animals, which live a very sheltered life, with abundant food and little in the way of danger or adventure. Hence we speak contemptuously of "the brains of a hen", in contrast to those of a crow in natural conditions, or even of a tame parrot, whose captivity is full of interest. In cases like horses and dogs, which become man's partners and share in his responsibilities, the domestication keeps the brain active, and there has, of course, been persistent selection in the direction of intelligence. We wish to linger for a little over the behaviour of hens.

Different breeds vary considerably, but expressions of intelligence are not common, and in many cases the hen seems to be distinctly stupid. It may fail, for instance, in the course of many weeks to learn the simple device of putting one foot on a loose lettuce-leaf, which is pecked at ineffectively because it is jerked away and often lost at every peck. A common interpretation is that the hen's brains have racially degenerated, either through disuse or because there has been no selection in the direction of intelligence. But in all probability this interpretation is wrong; first because it takes a long time for brains to undergo racial degeneration—evolution *up* and evolution *down* being slow racial processes; and, secondly, because of the very marked mental alertness of the chicks. What happens is an individual retrogression in the hen's lifetime, because the artificial conditions afford insufficient stimulus. Sufficiently awaken the need or the desire, as we shall see, and the hen's brain rises to the occasion—a Natural History fact of considerable importance.

If an instinct be an inborn, ready-made power of doing apparently clever things, then chicks have relatively few instincts—as com-

pared, for instance, with a young ant! It is true that almost from the first they can peck with precision at flies moving on the wall of the hen-run; that they can jump neatly from an eminence eight times their own height; that they can scratch their head with their toes; and that they have a few other instinctive accomplishments. But the remarkable fact is the smallness of their repertory. Chicks hatched out in an incubator paid no attention at all when their unseen and previously unheard mother clucked outside the door. They are not instinctively aware that the presence of a cat spells danger. Even when thirsty they do not instinctively recognise water, though they may be standing in a saucerful. They will stuff their crop once or twice with worms of red worsted—a very unprofitable meal.

Yet how quickly they learn to recognise four or more sounds which have "meaning" for them, to discriminate between profitable and unprofitable food-materials, to reject positively dangerous food, such as bees, and so on! There are few animals so educable as chicks—up to their limits. It is impossible to believe that there has been any racial degeneration of the brain in creatures so quick to learn; and it is very difficult to believe that educability disappears in the adult hen. More probably it simply falls into desuetude, because it is so rarely stimulated in a sufficiently interesting way.

This view is supported by some careful experiments made by Katz and Revesz. When they scattered mixed rice and wheat before their hens, they noticed that the grains of rice were always picked up first. So they tried a hungry hen with twenty rice grains which were glued irregularly to a slab of wood about five inches square; and between these they placed ten loose grains of wheat. At first the hen tried the rice grains, glued down quite imperceptibly, but could not detach them. It then picked up the grains of wheat. When all the ten were picked up, there was a rest for fifteen seconds, and then the hen got another similar lesson, and so on until it had seven. On each occasion the observers counted the number of pecks that the hen made before all the ten grains of wheat were swallowed. The figures are very interesting: 35, 19, 19, 16, 12, 10, 10. In other words, the hen had learned by the sixth lesson not to waste time over the rice grains. It inhibited and eliminated useless movements; and we have cited this case, which does not stand alone, not to show that hens are not so stupid as they look, but because it illustrates the value of educational methods that evoke interest.

(II*a*) HABITUATION OF INTELLIGENT ACTIONS.—An intelligent sequence of actions, requiring, to begin with, perceptual behaviour at many a turn may be repeated so often that it passes into habituation or enregistration. Practice makes perfect; and an intricate concatenation, as in the musician's triumphant skill, may

be achieved without detailed conscious control. At a lower level, yet often involving intelligent activity of considerable intensity, is the learning of a game of physical and psychical skill; and everyone knows how habituated this may become. As the word "habits" is used in several senses, e.g. for the whole behaviour of an animal and for pathological cravings, it may be well to keep the term habituation for the process and the result of enregistering intelligent activities until detailed control ceases to be necessary for their performance. It is plain that the results of training, though proving educability, are often much less intelligent than they seem. A good illustration is given by Hobhouse, who tells of the elephant that put pennies deftly into the slot of the biscuit-delivering machine, but rejected with impatience the halfpennies that would not work the mechanism. This looked on the face of it hugely intelligent, but it was the outcome of very laborious habituation, implying weeks of training, during which the trunk was guided to the automatic machine, and other weeks during which an associative discrimination of pennies from halfpennies was built up. It would be very extreme to say that there was no appreciation of significance on the elephant's part, but most of the performance depended on enregistering a sequence of acts. An association was established between the feel of the penny and raising the trunk to the slot, between the feel of the halfpenny and throwing it back to the visitor, but this did not involve even a spice of judgment. As long as the elephant was sensorily acute enough to distinguish pennies and halfpennies with the tip of its trunk, and plastic enough to establish a novel and very artificial neuromuscular linkage, there was no need for it to go farther in this particular connection. And we must be frank enough to admit that few of us know in any precise way how the disappearance of the penny is followed by the appearance of the biscuit, and why a halfpenny will not work.

When we turn from training that results in a routine performance to training which has its outcome in a variety of actions appropriately adjusted, we hear more clearly the note of intelligence. This is illustrated by an elephant's co-operation with the workmen in the forest, by the shunting horse at a railway station in the country, or, best of all, by the collie dog in its successful completion of a difficult piece of shepherding. In such cases the animal mind has been raised to a higher power by working in responsible partnership with man; and the most striking feature is the judgment shown in adjusting the response to the peculiarities of a particular situation. In the collie's case it seems that successful achievement depends not only on the individually variable educability, and on the shepherd's skilful training, but on the instruction given to the prentice by the parent dog, some say by the mother especially.

(III) **ASSOCIATIVE LEARNING.**—At a lower level than *intelligent* learning is what may be called *associative* learning, when the animal becomes, with more or less vividness, aware of the vital significance of some sight, sound, or odour. We are not referring to instinctive obedience to a specific danger-signal or the like, but to an association that is learned in the animal's apprenticeship to the life of the woods and mountains and shore. It means much for the animal's success in life to learn what certain sense-impressions stand for—whether danger or food or kin, and to be able to act accordingly. We refer to a grade of behaviour higher than that of the "conditioned reflex" to which we shall presently turn. Many a dog, when it hears a particular sound, such as the distant hooting of its master's motor-horn, will behave in a precise way, far above the level cf a reflex action. At a given signal certain fishes come to the bank to be fed; when a bird hears a certain note, it becomes excited and runs or flies towards the call. When the dry twigs on the forest floor crackle under a heavy foot, the squirrel darts up a tree. In the education of young animals by their parents, this process of establishing associations plays an important part. In the individual lifetime a certain stimulus comes to be associated with (*a*) the memory or enregistration of a particular previous experience, pleasant or painful, and (*b*) with a particular course of action. The psychical aspect is seen in the discrimination of the stimulus, e.g. a tell-tale sound from a non-significant one, and in the vividness of the revival of the previous experience. Frequent repetition brings about some degree of automatisation.

(IV) **PRE-INTELLIGENT LEARNING.**—At various levels of the Animal Kingdom, from the Protozoa upwards, one sees the pursuance of an apparently somewhat random "trial and error" method, in which the creature, in face of some difficulty, tries its various common movements one after the other, and may thus solve a problem. It is seeking satisfaction or the removal of dissatisfaction, and it goes through its repertory of movements. Here we have to do with endeavour, but not with intelligence. In any case, it is far below the level of the deliberately purposeful experiments made by the chimpanzee in trying to retrieve the fruit out of reach. Intelligence might be inferred if attention were arrested by the movement that proved effective, and if on subsequent occasions the profitless movements were more or less quickly eliminated. One of the lower monkeys wished to get a peanut out of a narrow-necked bottle and tried all manner of unintelligent shakings. Among these there occurred holding the bottle inverted in a vertical position, which of course attained the desired result. But this individual monkey had not the wit to notice what particular movement solved the problem; nor did its fortuitous success

lessen during the period of observation the number of subsequent failures. It is profitable to contrast this case with the way in which an untaught thrush, carefully observed by Miss Frances Pitt, learned to open its first wood-snail. In the course of a week it passed through the stages of indifference, interest, fumbling strokes, more effective thrusts, lifting the shell, and finally hammering it on a stone until it broke. But when it reached the solution which it had deliberately sought, it did not require any further experimenting. It had learned its lesson—along an intelligent line.

The term "habit" should be restricted to the *individual* enregistration of a novel sequence of actions, which require to be in some way "learned". In the sequence established, one neuromuscular action automatically calls up another, and that another, and so on; and it is easier that the links in the chain should follow one another than that anything else should happen. As people often use the words "habit" and "habits" with other quite different meanings, we keep the term habituation for the individually acquired enregistration, as well as for the process by which the enregistering is effected. There are two important points: (*a*) to distinguish habituation, which requires to be individually "learned", from instinctive capacities and reflex actions, which form part of the inherited organisation; and (*b*) to recognise that the habituation may be effected by non-intelligent as well as by intelligent repetitions of the same experience.

The difficulty of grading the different kinds of "learning" is illustrated by the ability many animals show in mastering a maze or labyrinth. This is often made like a miniature of Hampton Court's, and the animal is bribed to attention by a reward placed in the centre or at the doorway, according as the pupil learns to work in or out, or both ways. The maze can be mastered by monkeys, rats, mice, guinea-pigs, pigeons, tortoises, and so on; but wherein the process of "learning" precisely consists remains doubtful. Experiments have been varied so as to exclude the assistance of the senses of smell and sight; there is probably a memory of muscular movements. In a few days a docile rat will become quite familiar with the maze, and will scamper through it without blundering or even hesitating. After an interval of several weeks without any further maze-experience, a well-trained rat will run through the labyrinth without making any mistake, so that here again there is enregistration. A man might discern the particular rule or secret of the maze and keep that in mind; or a man might possibly form a mental picture of the perplexing paths; but we may be sure that what the rat does is something very different—something more physiological and less psychological. The probability is that it has a "kinesthetic sense" that enables it to remember the effective routine of movements. It must be noticed that these maze-solving creatures do not

learn in cold blood, but with an interested activity, whetted by appetite.

The "homing" of horses and some other mammals is probably kinesthetic; and as for cats that are transported to a distance in a basket, more precise information is required. One requires to know, for instance, the percentage of failures, and whether a cat that found its way in a few days from Ayrshire to Fife could have repeated the journey the following week. The "homing" power of ants and bees is in the main the outcome of learning the region and taking advantage of landmarks; the case of homing pigeons is by itself, since man secures a graduated education for the birds; the homing of migrant birds remains a puzzle. As indicated in another section, the experiments made with brooding terns, removed in closed baskets from the Tortugas and taken on board steamer for hundreds of miles into unknown waters, whence a variable percentage returned in safety, seem to prove conclusively that there is a "sense of direction" whose nature and location are quite unknown. All this, however, is but to emphasise the point that habituation is a very important factor, and that the "learning" process need not be intelligent. Very clear evidence of this is afforded by the behaviour of starfishes, which learn to free themselves more and more rapidly from staples which bind their arms to the experimenting table, of course without pain or actual contact. There is a gradual elimination of useless movements; but we dare not speak of anything like intelligence when we are dealing with animals that have not a single nerve-ganglion in their bodies. The nerve-cells are not integrated into centres. Nor, on the other hand, can we put our learning to ride a push-bicycle or to play a game like tennis at the simple level illustrated by the starfish, for although there is the important common feature of eliminating useless movements, man is continually demanding and receiving intelligent reasons for learning as he does. One of the clearest instances of non-intelligent "learning" is afforded by some experiments on earthworms which were confined in T-shaped tubes filled with soil, one path leading to a mild electric shock and the other to satisfaction. After 120–180 lessons, about six per day, the earthworms learned to avoid the electric path, making only one mistake or two out of twenty trials. But the lesson was learned not less thoroughly by *headless* earthworms! We need have no hesitation in this case in speaking of pre-intelligent learning.

Prof. Agar of Melbourne made some interesting experiments with water-fleas (*Daphnia carinata*), water-mites (Eylais and others), and the Australian freshwater crayfish (*Parachæraps bicarinatus*). Each animal experimented on was placed in conditions unfavourable to its normal activities, such as confined space, water too shallow to allow of unrestricted swimming movements, or with an excess

of dissolved carbon dioxide. In every case there were two apparent avenues of escape, one actually leading to freedom, the other ending in a *cul-de-sac*, so that a choice of this avenue brought no relief. In some cases the "unpleasant" result of making the wrong choice was made more emphatic by the administration of an electric shock, or by some other means. In most of the experiments the apparatus was a Y-shaped arrangement, the animal being placed in the stem of the Y, and having to make a choice between the left-hand or right-hand branch of the Y when it arrived at the bifurcation.

A dozen experiments with the water-fleas, involving altogether 1,400 lessons (the longest in any one experiment being 300), failed to disclose any power of learning by experience. The proportion of right to wrong choices showed no tendency to increase as the experiments proceeded. In the experiment in which one water-flea was given 300 trials or lessons, extending over eleven days, there were fewer correct choices in the last quarter of the experiment than in any of the other quarters.

Twenty principal experiments were made with the water-mites, the number of trials varying from 100 to 800, with a total of over 5,000. The first few experiments appeared to give positive results; but further tests, undertaken to confirm this, showed that while the water-mites have a well-marked tendency to form *motor habits* (tending to run for a long series of trials into the same passage), there was no good evidence of a power of learning. Some showed improvement during the course of the experiment, but others showed the reverse.

Very different results were obtained by similar experiments on young crayfish, for they very soon learned to avoid the wrong passage and take the right one. In one experiment, in which entry into the wrong passage, besides failing to bring freedom, resulted in an electric shock, the animal took the wrong (left) turn at its first trial, and then chose the right passage seven consecutive times. The electrodes were then put into the right-hand passage. The crayfish continued to go into this passage for 8 more times, receiving a shock each time. In the next 21 times it only twice entered this passage, making the correct choice in the other nineteen.

The interpretation Prof. Agar gives of the difference in educability between the crayfish and the other two animals is instructive. The difference may be correlated with the mode of life, for the crayfish searches for its food with sense-organs which are susceptible to stimuli from a distance. Having found its booty, it manipulates it with its mandibles and maxillæ. It will also defend itself with its great claws, and probably attacks other animals that might serve it as food. "Daphnia lives a life of far less initiative. It feeds on microscopic organisms, which are collected by a current of water produced by the movement of certain of its appendages. Presumably

there is no need, nor indeed much scope, for searching for food. Unlike the crayfish, Daphnia shows no evidence of awareness of other animals or bodies, except for an acceleration of the swimming movements when disturbed." The water-mites of the genus Eylais feed on water-fleas, which they catch as they swim. They seem to use no other sense than touch in discovering their prey. They rely on chance collisions for coming in contact with it. Thus the difference in educability is not merely that the nervous systems of the three types are at different levels—the brain of the crayfish easily the highest. Agar's suggestion is that the difference should be correlated "with the degree of psychological development required for the normal life of the animals".

(V) INSTINCTIVE BEHAVIOUR.—There can be no doubt that this term, though definable, covers some variety. Thus the behaviour of the female Yucca moth in pollinating the Yucca flower and laying her eggs in the ovary, is a complex linkage of instinctive acts, whereas the activity of the newly hatched Mound-bird in struggling out of the great heap of fermenting vegetation is more homogeneous, and more continuous. In the instinctive routine of ants, bees, wasps, and termites, intelligence is usually conspicuous by its absence; but in the ways of birds intelligence seems often to mingle with instinct.

What are the characteristics of instinctive behaviour, such as is familiar in the industry of ants and bees, in the spider's web-making, in the bird's nest-building and brooding? Physiologically considered, instinctive behaviour is a concatenation of reflex actions; in other words, there is an inborn predisposition of certain nerve-cells and certain muscle-cells—part of the hereditary constitution, just as much as are the neuro-muscular arrangements which regulate the effective beating of the heart. And in what we have just said, it is implied that the instinctive behaviour does not require to be "learned" by the individual animal. The first web constructed by a spider is usually true to type; a larger and stronger web may be made later on, but the pattern of the first one is the pattern characteristic of the species in question. Yet the characteristic "ready-madeness" of instinctive behaviour must not be over-emphasised; for the animal sometimes becomes more effective as it becomes more experienced. Another feature involved in the innateness of instinctive skill is its equality in all members of the species of the same sex. There is little hint of the individual variability that is often so marked in intelligent behaviour.

From the frequent perfection of instinctive behaviour, it almost follows that it must have remarkable limitations. The pre-established neuro-muscular arrangements necessarily bind the animal to a considerable routine. Instinctive behaviour is often extraordi-

narily stereotyped or obligatory; and it has often been remarked of ants, bees, and wasps that hardly less wonderful than their achievements are their limitations. Thus the ready-made efficiency of instinctive behaviour is apt to bring with it the handicap of tyrannous adherence to routine. But this again must not be exaggerated, for there are many instances of *modified* instinct, as when a spider constructs a web in a peculiarly difficult situation, or when ants are confronted with some artificial difficulty, such as a tarred band around the bole of one of their trees. In such cases the probability is that a spark of intelligence illuminates the situation, and so sets the instinct free to its work again.

Looked at ecologically, rather than physiologically, instinctive behaviour is always related to particular circumstances, which are either of frequent recurrence, or are such that an effective response to them is of critical moment in the survival of individual or species. Intelligence, as we have seen, implies some psychical appreciation of relations, and is not necessarily definitised in its reference; but instinct is always definitely related to particular circumstances. If an ape has learned the use of a small lever, it may proceed to make a large one; but this intelligence is conspicuous by its absence in the field of instinctive behaviour, the triumphs of which in honeycomb and in wasp's nest, in the water-spider's sub-aquatic dome and in the termite's tower, are none the less astounding. When we think of the difficult problem of the evolution of an instinct, the particular definiteness of its reference must be kept in mind. Whatever be our theory of the origin of any of the marvellous instinctive capacities, can we avoid the conclusion that it was *tested* by generations of individuals in relation to a particular kind of environment and need?

But in varying degrees there is also a psychical aspect to instinctive behaviour—a proposition which requires some proving. For it will not suffice to fall back on the more vague panpsychic proposition, true though it be, that every integrated physiological sequence has its psychic side. Evidence must be brought forward to show that we cannot make sense of instinctive behaviour without postulating a psychical factor. The chain of reflexes is suffused with an awareness that is more than sensitiveness to stimuli, and backed by an endeavour that is more than appetite. We may not be able to demonstrate the reality of this psychical accompaniment as we can demonstrate the electrical change that is associated with every contraction of a muscle and every secretory activity of a gland. But we must at least show that the psychic postulate is necessary for clear thinking or adequate description. This involves the consideration of numerous instances, and these we can only sample.

To sum up so far: in instinctive behaviour we are dealing with a range of activities that are predominantly the outcome of racial

enregistration. They are on different lines from intelligent behaviour, which implies initiative and tentative. An instinctive action is like a reflex action, but at a higher level, and with more psychical accompaniment; both depend not on a generalised ability for judgment and appreciating relations, as in intelligent behaviour, but on engrained or enregistered predispositions which are capacities rather than abilities, requiring only the liberating stimulus.

INSTINCTIVE BEHAVIOUR OF TAILOR ANTS.—As a useful illustration we take the tailor-ants, which have been often studied since Ridley first described them in 1890. The essential feature is the binding of leaves with silken threads so that a nest is formed which serves for the shelter of the eggs, larvæ, and cocoons.

A first impression is that many grades occur between rough-and-ready structures and astonishing masterpieces; and the obvious lesson is that if the masterpieces alone had survived, the possibility of giving an evolutionary account would have been very remote. It would be a task as hopeless as trying to give an account of the evolution of the human ear, with all its extraordinary intricacy of minute structure, if it were the only surviving ear. When all the many grades of ear are taken into consideration the evolutionist's task is not so hopelessly difficult. Thus in regard to the tailor-ants, Forel tells us that in many cases the silk threads form little more than a tangle binding several leaves together, and providing a simple shelter within which the queen ant lays her eggs and the workers attend to the young ones. It is said that the fruit-growers in the Far East like to have these tailor-ant tangles about their trees, for they believe that the industrious ants capture appreciable numbers of injurious insects. But our present point is merely that the series of nests begins with very simple forms—a long way from the masterpieces. In the common Tailor-ant (Œcophylla), which is widespread in warm countries, what happens is as follows:

A number of workers combine their forces to draw two leaves together. The margin of one leaf is seized by the mandibles and the margin of the other is gripped by the three pairs of legs. If the gap from one leaf to another is too great to be bridged by one ant, a living chain is formed, somewhat like what we occasionally see among those gymnasts who take our breath away. Ant *A* grips the leaf with its legs and grips ant *B* in its jaws, seizing it by the narrow waist. This allows *B* to grip the other leaf with its jaws. But if *B* cannot reach the leaf, it takes *C* in its jaws; and then the chain has three links. We do not know what the maximum number of living links is, but one traveller has told us that he counted six. In any case, even with two or three links, the feat is very remarkable; and as it is not habitual, it may illustrate the intervention of intelligence.

But this is only half of the story. While the tug of peace is going on, other workers get hold of larvæ, gripping the soft body of the grub by the middle. Now, the grub of an ant has got what the parent has lost—namely, a couple of silk-glands opening at the mouth. The ordinary use of these is to form a silken cocoon, within shelter of which the grub changes into an ant. The cocoons, or pupa-cases, are popularly called "ants' eggs"; but this is, of course, very bad natural history. The cocoon-making is usually finished in one day, and the glands do not need to be very large; but in the grub of the tailor-ant they are unusually big and can make a lot of silk. So it has come about that the worker-ant with the grub in its mouth is able to dab it against one leaf and then carry it over to the other leaf, thus drawing out a thread of glutinous silk.

Several workers do this over and over again, and the result is a sort of web of silk binding two or three leaves together. Some naturalists have compared the silk-producing larva to a shuttle and the worker to a weaver; others speak of the larva as the worker's needle and thread. In some ways it would be nearer the mark to say that the larva serves as a living gum-bottle. But the result is a web, an essential part of the nest.

In contrast to the rough-and-ready nest-tangles, there are masterpieces. Thus Forel has in his collection a triangular tree-nest about eight inches high and six inches at the base, a substantial but very light construction woven among the leaves. The detailed architecture is extraordinary, for the nest consists of a large number of adjacent and superposed compartments, each a little under half an inch across and about a fifth of an inch in height, all bound together by minute pillars and beams. This would be striking enough if it were made of chewed wood or salivated earth, after the fashion of the termitaries which the so-called "white ants" construct. But this masterpiece is woven out of silk. It would be striking enough if it were made by a spider, though their webs are often triumphs of instinctive art. But the spider makes its own silk, whereas this so-called tailor-ant is using its larvæ all the time!

Dr. Goeldi, who found the nest in Brazil, noticed the workers repairing some compartments that had been slightly damaged, and each had a grub in its jaws. A very quaint detail was that the nest included another nest, which belonged to a minute bee. The ants had simply included the bee's tiny construction between their own nest and the leaves of the branch. The association seemed to be quite amicable, "wheels within wheels" again. Forel calls it "pacific parabiosis", but by any other name it would sound as surprising!

Among the most striking tailor-ants are the large and handsome members of the genus Polyrhachis, deserving a more usable name. Some of them have a golden-yellow breast and a burnished-black hinder body; others have a burnished-black breast and a golden-

yellow hinder body, and others are old-gold all over; for so the changes are rung among species. But we are concerned just now with the nests. One of them, from Java, consists of many compartments, as in the preceding nest from Brazil; but the workers have utilised the silken web as a basis for intermingling minute fragments of leaf and stem and bark. The result is a flexible brown contraption, half silk, half debris, sometimes among the leaves of a palm, and sometimes among the grass.

In this case the ants are not carnivorous like those we started with; but they keep small coccus insects as domesticated animals, and use the surplus nutritive materials of these "cows" as part of their own sustenance. Jakobson, who noticed this in Java, found little stables beside the main nest—the byres for the cattle. And these little stables have also their silken foundation, furnished by the larvæ.

It is interesting to notice the great variety of nests in this one genus (Polyrhachis) of handsome tailor-ants. Some consist entirely of woven silk; some have fragments of plants added to the silken web; some have a silk fabric which serves as the foundation for a superstructure of papier mâché. In some species the nest is a one-roomed house; in others there are numerous rooms. There are also miniature nests, less than an inch long and hardly half an inch broad, almost as simple as sleeping-sacs, but covered outside with greyish lichen. One could almost predict where they are found—pressed against the bark of a tree. Everywhere we get the impression of living creatures as experimental, proving all things and holding fast that which is good. For all the kinds of nests that we have mentioned in this section are made by species of one genus. This is *specificity* in behaviour.

But the most remarkable fact, after all, is the central one, that the worker-ants use their baby-sisters to make the silken web. Whether we compare the larvæ to shuttles, or to needle and thread, or to animated gum-bottles, the fact stands out that the workers are using other creatures—their own kith and kin, to be sure—as tools. Do any other creatures besides man utilise other living creatures as tools? Is this a unique case?

Everyone would like to know how the strange custom arose. Even if we emphasise the fact that ants are, in the main, children of instinct, we may suppose that individuals put inborn non-intelligent inspirations or initiatives to the test of experience, and stick to those that pay. It is probably safe to conclude that the utilisation of the larvæ did not occur to the ancestors of the tailor-ants as a bright idea. This is too generous. It is more likely that the custom arose as an extension of something else, and was adopted after it was tested. That something else might be, as Forel suggests, the custom that ant-workers in general have of cleaning the cocoons

and removing adherent particles. There is also the fact that the silk thread that issues from the larva's mouth is sometimes very sticky, and readily adheres to other threads and to adjacent fragments. Then there is the custom of moving the cocoons about from place to place when there is danger or need of sunshine. In some such way the "tailoring" may have arisen. But the beginning of this story may probably remain a perhaps.

LINKED INSTINCTS.—The effectiveness of instinctive behaviour depends (1) on the fact that the efficiency is part of the hereditary equipment, not requiring to be learned; (2) on the automatic readiness with which the response comes to a stimulus, without hesitancy or fumbling; and (3) on the linking of one group of reflex activities to another, so that the completion of *A* serves as the stimulus to the commencement of *B*, and so onwards. This idea of "chain-instincts", as they have been called—perhaps linked instincts is clearer—deserves illustration.

In birds, for instance, the instinctive activities connected with reproduction follow one another in a definite harmonious series, modifiable, however, by intelligence to a degree unknown among insects. As Herrick suggests in his luminous essay on the cuckoo, the instinctive bird-cycle may be graphically represented by a number of nearly tangent circles, each of which stands for a distinct sphere of influence or for a series of related impulses. Perhaps it is enough in the first instance to think more objectively of each circle as a group of reflex activities. They are conditioned, no doubt, by external influences and internal impulses, but these are in most cases very imperfectly known. We are not at present raising the question of the degree of awareness and endeavour behind the behaviour.

The cycle varies for different birds, but the commonest sequence, adopted by Herrick, is:

1. Migration (often followed by choice of "territory");
2. Mating (with often complex courtship);
3. Nest-building;
4. Egg-laying in the nest;
5. Incubation and care of eggs;
6. Care of young in the nest;
7. Care and education of the young out of the nest;
8. Scattering, and migration anew.

A group of reflex activities may include many often-repeated linkages of reflex acts (physiologically considered), as in nest-building; or it may be very monotonous, as in close incubation; and each continues, with what we may metaphorically call "momentum", until there is a change in external influence or in internal impulse. Thus the hatching out of the young birds is a liberating

stimulus which evokes changes in the behaviour, such as the interruption of the close brooding by excursions for food. The bird's prolonged sitting on addled eggs is not a mark of stupidity; it merely means that the stimulus leading from circle 5 to circle 6 has not been forthcoming. Many anomalies in the reproductive behaviour become more intelligible in the light of the idea of chain-instincts. One term in the series may be weakened, or even dropped out, if the stimulus to the next term comes into operation prematurely, or if the stimulus to the antecedent term be continued for an unusually long time. Thus the cuckoo, highly sexed and polyandrous, has a prolonged sex-urge, and has suppressed nest-building and all that follows. Or more generally, we may say with Herrick that the normal cycle may be disturbed so that there is a lack of attunement. Thus many an individual bird drops its eggs casually on the ground, the nest-building instinctive activity remaining dormant or awakening too late.

Many a bird, especially a male, may build two or even more nests, instead of being satisfied with one; the third circle has usurped more than its normal share of the time and energy available during the short reproductive period. Occasionally the autumnal migrating instinct is awakened prematurely, and the parent birds leave their offspring to perish. As to the causes of the disturbance or lack of attunement in the normal sequence, they may be looked for in some nervous, endocrinal, gonadial, or other variation affecting the outcrop of impulse, or in some unusual vicissitude in the environmental conditions or in the pairing.

YUCCA MOTH.—One of the best-known instances of chain-instinct is the behaviour of the Yucca Moth (*Pronuba yuccasella*) when it visits the beautiful Yucca flower (*Yucca filamentosa*) and effects pollination. The facts were clearly described by Riley (*Reports Missouri Botanic Garden*, 1892, pp. 99–158, figs.), and are in several ways very instructive. The Yucca is one of the Liliaceæ, and produces (sometimes at intervals of years) tall spikes of creamy flowers, one or more of which opens every evening or so for several weeks in succession. It is a night-flower and gives forth a pleasant fragrance, which attracts the female Yucca Moth, without which there can be no fertile seed. None is formed in the Yuccas that occasionally flower in British gardens.

The female Yucca Moth, emerging from her pupa-case into a world of which she has had no experience, becomes fertilised, and thereafter flies to the freshly opened Yucca flowers, and collects pollen from the stamens. She uses her peculiarly shaped maxillæ, and holds a little ball of pollen by means of two sickle-shaped maxillary tentacles in front of her head. She then lays an egg in the ovary, but usually in that of a different and older flower. Having deposited the egg, she carefully places the ball of pollen on the

stigma, and the down-growing pollen tubes effect the fertilisation of the ovules—usually by cross-fertilisation.

The Yucca Moth proceeds to repeat the sequence: visiting a flower, collecting pollen, making a ball and holding it, visiting another riper flower, laying an egg in its seed-box, depositing the pollen-ball on the stigma, and then flying off to begin anew. It is evident that there are some six links in this instinct-chain.

The egg of the moth develops in the seed-box, and the larva feeds on some of the seeds which would not have grown if the ovules had not been fertilised. As there are far more seeds than the larva requires, the linkage works well for the plant as well as for the insect. What we are concerned with here is the chain of activities, but we may digress to notice two interesting points, illustrative of the "wheels within wheels"—the subtlety of these inter-relations. The Yucca, as we have mentioned, does not flower every year; and it is remarkable that there is in the Yucca Moth family (Prodoxidæ) a variability in the length of time that is passed in the pupa-state. The quiescent phase sometimes lasts a year or two longer than usual! We do not, of course, say that moth and plant keep time with one another in their respective emergence and flowering; but it is striking that both should be variable. Fine weather conditions probably favour the simultaneous appearance of the moths and the flowers in the same year; but in their native haunts in south-western North America there is probably some flowering and some emergence of moths every season. None the less it is very remarkable and unusual that one particular species of plant and one particular species of insect should be absolutely bound up with one another in the continuance of their respective generations.

The other linkage concerns another genus of moths (Prodoxus) which also lays its eggs in the ovary of the Yucca flower. With this great difference, however, that the species of Prodoxus have not the mouth-parts characteristic of the species of Pronuba and are therefore unable to pollinate the Yucca. But without pollination the ovules do not become seeds, and the ovary does not grow larger. Thus it follows that this "bogus Yucca Moth", as it is called, is dependent indirectly on its relative the "true Yucca Moth"; Prodoxus is dependent on Pronuba. But let us return to further illustration of the linking of instincts.

LAMB-THEFT.—A suggestive illustration, worked out by Mr. A. H. L. Fraser (*Journ. of Psychol.*, 1926), concerns the lambing instincts of Cheviot sheep. Two saving clauses may be emphasised at the outset: (1) That here, as with birds, there is a frequent mingling of intelligent control with instinctive routine; and (2) that the behaviour

varies considerably in different breeds, and may even be modified in the course of the individual lifetime.

The ordinary sequence is the following:

(1) Isolation.—When the sheep is near the time of parturition, it separates itself from the flock; and it is well that it should be allowed to do so. There is a search for a suitable place for the birth, and in many cases, under modern farming conditions, this is unimportant, for all the available places are much the same.

(2) Scraping.—Having found a suitable place, conveniently a slight depression, the sheep scrapes with her fore-feet alternately. There can be little doubt that this is an outcrop of a practice established under wild conditions. In most cases it is quite futile to-day.

(3) Parturition.—The next chapter is the actual giving birth; and it is of interest to contrast the behaviour of the gimmer (giving birth for the first time) with that of the ewe of two or three years' experience. The gimmer is in many cases puzzled by the appearance of the lamb, sometimes actually afraid of her offspring. Even in the domain of instinct, experience may count. The experienced ewe is a better mother than the gimmer.

(4) Licking clean.—The next step is licking the newborn lamb, and it seems to be the taste of the amniotic fluid that liberates the maternal instincts. If the mother has once licked her lamb, she will not let it go; but if she does not lick and cannot be induced to do so, she is likely to forsake her newborn offspring. After the cleaning begins the suckling, and soon there is the return to the flock.

Now if something occurs to perturb the normal sequence of chain-instincts, things go wrong; and a good instance is "lamb-theft". This is a familiar occurrence when the sheep that has not yet given birth, but is approaching her time, licks the newly born lamb of a neighbour ewe—her isolation not having occurred. The result is that she adopts or steals the lamb which she has licked; and this "misplaced affection" may be fatal to her own offspring. Mr. Fraser interprets lamb-theft, convincingly we think, as the result of the artificial conditions of the farm, which may allow the sheep thus to get a taste of amniotic fluid prematurely. This liberating stimulus should normally *follow* parturition; if by chance it precede it, then the mothering instincts are awakened before the proper time, and the result may be lamb-theft or worse.

This conception of instinct-chains or concatenations also illuminates other cases we have discussed, such as Fabre's case (p. 622) of the emergent mason-bee grub, which, after biting its way through its own firm larval case, remains finally imprisoned by an artificially added film of paper.

Apprenticeship of the Worker-Bee.—As a corrective of the impression of tyrannous automatisation that we get from some

examples of instinctive behaviour, it is useful to take account of Rösch's precise study of the gradual change of behaviour in worker honey-bees. By marking individuals in an observatory hive he was able to follow the apprenticeship of the worker-bees and their gradual promotion, so to speak, from one kind of duty to another, in the course of their short summer life of a month or six weeks. The newly emerged workers are turned to the task of preparing and cleaning wax cells in which the queen will lay eggs. After a few days they pass, or are promoted, to the status of nurses, watching over the young bees in their cells. At first they attend only to the older larvæ, supplying them with pollen and honey which other workers bring in; but later on they are allowed to look after the very young larvæ, which require a special nutritive fluid secreted by their nurses. This milky fluid comes from the upper pair of salivary glands in the head, which begin to function at this time, about the tenth day of winged life. They are not developed in queens or drones. A few days later, when the worker has been at work for about a fortnight, she leaves the brood-comb, or "nursery", and spends a week in the general service of the hive—in cleaning away refuse, distributing and storing food, and in similar duties. Trial flights in the open may also be made, but on these first ventures no pollen or nectar is collected. Finally, at the age of about three weeks after emergence, each worker is assigned the last of its indoor tasks, that of acting as guardian at the gate, preventing the entry of strange bees or other insects. Having duly discharged this duty, the worker-bee devotes all its remaining time and strength to the work of collecting nectar and pollen from the flowers. But here, as Frisch has proved in detail, confirming Aristotle's observation and Darwin's remark that "bees are good botanists", there is often a singularly monotonous efficiency. For when a bee has found a profitable and abundant species of flower, it may keep to that for the whole of its short outdoor life without ever entering another kind of blossom.

As Rösch is a scrupulous observer, his account of the bee's succession of activities must be carefully considered. There are several points of importance. First, there appears to be a social control which leads the worker from task to task, though there is also the physiological change, as in the activation of the salivary glands, which makes the bee fit for a particular task when she reaches a certain age. Second, there is the occurrence of trial flights in the open before any actual collecting begins. This suggests that the bee must not be thought of too mechanically, as if it were an automatic machine compelled by the release of successive springs to a definite series of activities. Thirdly, there is here a good illustration of the economising of energy that is made possible by a social organisation. Every day of the short life is utilised by the graded succession of duties.

Limitedness of Instinct.—One of the pronounced characteristics of instinctive behaviour, as contrasted with intelligent behaviour, is its *limitedness*. While it may be in varying degrees suffused with awareness and backed by endeavour, it evidently does not include an intelligent appreciation of the situation. Thus the animal may continue an instinctive activity after it has ceased to be relevant, or may engage in some task which is futile because premature.

In some cases an animal has been misunderstood even by experts, and called "unutterably stupid" because of its bewilderment before some serious disturbance of the ordinary instinctive routine. Whitman studied the varied behaviour of different kinds of pigeons when the eggs were removed during the brooding bird's brief absence and were placed a couple of inches or so outside the nest. Some kinds retrieved the eggs, some were satisfied with one egg, some made not the least effort to recover what had been removed but sat patiently on nothing until the brooding instinct waned away. But it is a mistake to think a creature stupid when it fails to cope with the disturbance of a routine that is normally quite instinctive. When a department of normal activity, such as brooding, has been, so to speak, relegated to instinct, i.e. has come to be adequately discharged by a chain of inborn neuro-muscular predispositions, and sometimes habituations as well, then it is apparently difficult for intelligence to intervene, though it may be more or less clearly exhibited in other situations where the animal is untrammelled.

A few examples of the limitations of instinctive behaviour may be recalled. When the Procession Caterpillars, a plague of the Mediterranean pine-woods, are full grown, they descend from the trees and go on the march. They form an Indian file, head to tail, and go straight on until they find earth soft enough to allow of burrowing and pupation. Fabre adjusted the length of a file so that it extended round the stone curb of a large circular water-basin in his garden, and brought the head of *A* into contact with the tail of *Z*. The well-known result was that they continued for a week in futile circumambulation, when a little spice of judgment would have broken the spell. Yet does not even man too often show something of the like—enslaved by habituation, if not by instinct?

So the lemmings on the march, obedient to their instinct to go straight on, may swim out in large numbers into the sea and thus meet their fate. So when the opening of the ground nest of the common wasp is covered with a bell-jar, the imprisoned insects never dig a passage out, though they readily could if they had the sense to try. They are not physically imprisoned, but physiologically and psychologically. Stragglers from outside may dig their way in,

but they cannot come out again, far less show their fellows the way! Instinct is thus essentially fatalistic.

Take another case from Fabre's repertory. The mason-bee makes a cylindrical mortar nest, with a lid through which the mature grub bites its way. If the lid is artificially thickened by glueing on a little disc of paper, the grub has no difficulty in cutting through the extra thickness. But if a paper cap be fixed on, like a pill-box inverted, just a little way above the natural lid, but not in contact with it, the grub, emerging into the closed space between the natural lid, which it has cut through, and the artificial cap, which it could, physically, easily cut through, is nevertheless inhibited fatally. When it has emerged into a free space the cutting instinct ceases and cannot be roused again. The grub dies in its paper prison—for lack of the least glimmer of intelligence to take the place of the satisfied instinct.

Very interesting ecological observations, at a high level of carefulness, have been made by Portielje in the Amsterdam Zoological Gardens. Thus he has studied the once common, now sadly dwindling, South American ostrich Rhea; and one of the general facts that he brings out very clearly is the high reach and yet limitedness of instinctive behaviour. When the cock has begun to sit on a few eggs in the shallow depression that serves as a nest, he likes to be visited in natural conditions by members of his harem—in the Amsterdam case, by his one and only wife. She seems half-hypnotised as he stares at her with extraordinary intentness; and she lays an egg close by the nest. Whereupon the brooding cock uses his flightless wings, his bill, and his feathered neck to draw the egg under his body. In a very remarkable way he makes a hook of his neck and adds another treasure to his store. Yet "treasure" is not, strictly speaking, an admissible word, since we know that, before the cock-bird has begun to brood, he passes a dropped egg with nonchalant indifference. A single egg lying anywhere has no meaning for him; in any case, it does not serve to pull the trigger of the incubating instinct. But this impulse asserts itself when he sees an egg, or better still several eggs, in the so-called "nest". Then he begins to brood assiduously, and the eggs—which may eventually number a score—become never-too-much-to-be-sat-upon objects. On the one hand, there is high development of an instinct; on the other hand, remarkable limitedness.

Another instance may be given. When an egg hatches early, before the brooding instinct is waning, the cock rhea is puzzled by the appearance of the nestling. Who is this little stranger? The cock bird, preoccupied with sitting, has no notion of kith and kin, so he sometimes throws his firstborn offspring away! He may do the same with number two. How extraordinarily limited! Yet in a short time, when more nestlings are hatched out and the incubatory instinct

wanes, the cock rhea becomes a careful and courageous father, not to be separated from his offspring, to whom he is as good as a mother. How limited, and yet how high!

For obvious reasons there is not much parental care among fishes; yet it is sometimes exhibited in a high degree, as in Sticklebacks and Bubble-fishes, especially when the number of eggs is relatively small and when there are many chances of death in early life. For weeks the fish—usually the male—may guard the developing eggs, fasting all the time; and surprise has been expressed that this should sometimes end, in aquarium conditions at least, in the offspring falling victim to the parental appetite. Here, again, there is apt to be misunderstanding, for the instinct to seize a rapidly moving object, after being inhibited for a period by a strong parental instinct, not unnaturally reawakens when the cradle empties and the parental instinct dies away. In natural conditions there is usually a rapid scattering of the progeny.

Very instructive, again, are the experiments made by Mayer and Soule on the caterpillars of the common milkweed butterfly (*Danais plexippus*). When the caterpillars have started eating, they may be induced to accept leaves which they would never have begun with. "The momentum of the reaction"—to munch—carries them on, though the proper taste and smell stimulus, without which they will not *begin*, is absent. The observers note, however, that the tyranny of instinct is not absolutely rigorous. If a "distasteful" leaf is presented at intervals of about thirty seconds, the caterpillar takes fewer and fewer bites, and then refuses altogether. It is beginning to learn. Yet if the distasteful leaf is offered at intervals of a minute and a half, the caterpillar tries it every time and takes about the same number of bites. Its associative memory is very short. Yet there is a hint here that instinctive predisposition may serve as the firm foundation for an improved superstructure of behaviour, the outcome of experience. But the paradox seems to be that the firmer the foundation of instinct, the more difficult it is to build on *intelligently*. Yet some of the instances we have given, such as that of the rhea, and the milkweed caterpillars, seem to us to show that the eking out of instinct by intelligence is undeniable.

In emphasising the limitedness of instincts—a familiar fact to the field-naturalist—we must not fall into the error of thinking of them as rigidly stereotyped. Their variability has largely stopped, because so perfectly adaptive, but it has not *necessarily* stopped. Variations which express themselves in an improvement of the nervous system, such as those which deepened a convolution in the Carnivore's cerebrum, or increased the size of the neopallium in the early Primates, cannot have been without their counterparts in the evolution of instincts. Apart from inferring this from the gradations that occur in different species and genera of social insects, we have

records of variations in the instinctive routine of the same species. From the nature of the case we cannot expect them to be numerous, like variations in intelligence.

When cerebral variations—say improved differentiations and integrations—occur in predominantly instinctive types, they must, if they are to count for anything, be tested and sifted in the individual experience, so that we must recognise some initiative or tentative activity abetting the process of racial enregistration. The neural improvement or new departure is, so to speak, a particular card in the individual's hereditary "hand"; whether it will add to the racial stability or not depends on how the individual plays that card. This is the tentative side of instinct, and one of the conditions of its evolution.

INTELLIGENCE AND INSTINCT CONTRASTED.—Many years ago Ray Lankester drew a clear distinction between (*a*) the "little brain" type, reaching a climax in ants and bees, with a rich repertory of instincts and very little power of educability; and (*b*) the "big brain" type, reaching a climax in the highest Vertebrates, with relatively few instincts in the strict sense but with remarkable powers of learning or profiting by experience. From a different angle Bergson reached the same general conclusion, that instinctive and intelligent behaviour are on different lines of evolution, each with its own advantages and disadvantages. But these two great kinds of behaviour do not admit of very close comparison, still less of being pitted against each other.

It is useful to dwell for a little on the contrast between instinctive and intelligent behaviour. Instinctive behaviour requires no learning, but intelligent behaviour is based on what the naturally nimble brain learns. The newly hatched mound-bird, having struggled out of the egg-shell, has to continue to struggle out of the great heap of fermenting vegetable debris. If it stops to think, or through fatigue, it perishes. If it continues its instinctive struggles it wins its way through, and hurries into the scrub. The Yucca Moth, as we have seen, makes no tentatives; how different from the song-thrush with its wood-snail!

Instinctive capacity is shared equally by all members of the species of the same sex, whereas intelligent capacity varies greatly from individual to individual. All female spiders of the same kind make an equally perfect web. Of course one must not make a dogma of this perfection of instinct; for mistakes are sometimes made, when the consecutive manipulations are very intricate. Fabre tells us of the Calicurgus wasp that stings its captured spider near the mouth, thereby paralysing the poison-fangs; and then, safe from being bitten, drives its own poisoned weapon into a thin part of the spider's cuticle between the fourth pair of legs. But it seems that the precision of the thrust is not always perfect.

If an instinctive capacity implies, on its physiological side, the gradual elaboration of a number of neuro-muscular linkages, activated by particular stimuli of vital importance, we can understand its characteristic limitation that it ceases to work well when there is some upsetting change in the circumstances.

If instinctive behaviour implies the hereditary or racially established neuro-muscular prearrangements for a series of reflex actions, in which *a* serves in part to activate *b*, and *b* does the same for *c*, and so on, then the higher animals of the big-brained type do not show very much of it. Educability and instinctive capacity are in inverse ratio. A chick usually degenerates into an over-domesticated hen; but it is in its youth alertly intelligent and astonishingly quick to learn. With this is associated a paucity of instincts in the zoological sense. If hatched out in an incubator it does not recognise its mother's call when she is brought outside the door of the room; it does not recognise water as water, although it walks through a saucerful and will greedily swallow if a drop suspended from a finger-tip is brought into touch with its bill; it will stuff its crop with unprofitable worms of red worsted! But these and a score of other significances are very rapidly learned.

EXTRAORDINARY "DEVICES".—The suggestion of intelligence, as distinguished from inborn instinct, sometimes comes from the extraordinary subtlety of what the animal does. A spider's beautiful web commands our admiration, but it is almost demonstrably instinctive—made true to type the first time and made sometimes in the dark; and there are more striking feats than making a web. Longman describes a Queensland spider called "the Magnificent" because of the particularly fine colouring of the female. But it is her way of catching moths that interests us most at present. She hangs down from a line and spins a thread about an inch and a half in length, bearing at the free end a globule of very viscid matter, a little larger than the head of a pin. The thread is held out by one of the front legs, and on the approach of a moth the spider whirls the thread and the globule with surprising speed. The moth, which seems to be attracted, is struck, caught, pulled in, killed, and sucked. When it is touched by the whirling globule, it is as helpless as a fly on fly-paper. The ingenuity and originality of the device cannot but arouse our admiration; we may well say of the Magnificent Spider "c'est magnifique!"; but how difficult to think over the performance without giving the creature credit for controlling awareness!

A very interesting fact, confirming the induction that good brains run in families, is the recurrence of somewhat similar behaviour in a related South African species of spider, also handsome and large in its female expression. To a horizontal line the female spider fixes a thread of silk with a viscid globule at the free end, and this is held out by the third or shortest leg. But, unlike its Australian

relative, this South African spider does not wait for the appearance of a moth at which it may hurl its globule, as the horseman his bolas; for what she does is to anticipate events by whirling the globule round and round in a horizontal plane, though there is no booty in sight. It must be noted in regard to both observations that spiders generally are very short-sighted. In any case, the fact is that the African spider keeps whirling her globule round, minute after minute, even for a quarter of an hour without stopping. Pausing then, if she has been so long unsuccessful in catching a moth, she draws up the thread and swallows the viscid globule, for it loses its stickiness after prolonged exposure to the air. After a short rest she makes another globule and repeats the extraordinary performance, which is sooner or later rewarded by catching booty. Neither of these two spiders makes an insect-catching web—not at any rate during the cocoon-making season, to which the observations were restricted.

Whatever the definitions may be, there seems no doubt as to there being a real difference between instinctive and intelligent behaviour. But it does not follow that an animal predominantly instinctive cannot also act at times intelligently, or that in the course of instinctive behaviour there may not be an interpolation of intelligent control. How should we know if such interpolation occurred?

As a rough-and-ready test among animals of "the little-brain type", such as ants, bees, and wasps, one may say, as already explained, that instinctive behaviour is marked by its routine character, by being performed with a considerable degree of perfection the very first time, by being shared equally by all members of the species of the same sex, and by remarkable limitations when something goes a little agee. Our question is whether we can find convincing instances of the interpolation of another kind of behaviour, which we cannot describe without giving the animal credit for some understanding of the situation, some perception of relations, some perceptual inference. We submit the following observations by Rau as a typical case of what we mean. One of the hunting wasps, a species of Pompilus, is in the way of pursuing trapdoor spiders. It opens the silken-hinged lid of the shaft and descends; it stings its victim and drags it above ground to its own nest—to serve in a paralysed condition as part of the larder of fresh meat for the wasp-grubs when they are hatched. So far there is nothing very remarkable, as wasps go; but let us continue the story. When the autumn comes, the trapdoor spider in question makes a second shaft to her burrow, diverging at an angle, and opening by a door on the surface not far from the original entrance. It is no longer so easy for the Pompilus wasp to catch its spider; for the burrower may escape by the second door, while the wasp is entering by the

first. Pompilus has three devices, and this possibility of alternatives leads us to look out for intelligence. Its first device is to break off the doors—a proceeding that brings the spider up to try to repair the damage. The spider is then caught. A second device is to insert its tail in the first entrance and then withdraw it, keeping an eye meanwhile on the second door by which the spider is likely to try to escape. The wasp's third device is to rap first at one door and then at the other, until the spider becomes excited and makes a rush. But the wasp is almost invariably too quick for the spider. The ingenuity and variability of its behaviour must be regarded as indicative of intelligence. There seems to be a plastic appreciation of the situation.

While the instinctive is an expression of non-intelligent racial enregistration, and does not necessarily require any "learning" or understanding, one must not think of instinct and intelligence as quite separate entities or faculties. The whole life is a unity, and one must think of instinctive behaviour as possible without much mental correlate, whereas "mind" is the true inwardness of all behaviour that is worthy of being called intelligent. What is inherited in the predominantly instinctive animals is a set of neuro-muscular predispositions of a very precise type, yet accompanied, no doubt, by a stream of feeling, as well as by a certain degree of awareness and the bent bow of endeavour. What is inherited in the predominantly intelligent animals is a highly developed brain, and the correlated mental aspect of imaging, experimentation, memory, and enjoyment.

(VI) **RHYTHMS.**—It seems useful to group by themselves what may be called enregistered rhythms, where there is a periodic expression of a particular kind of activity. The well-known Planarian worm called Convoluta ascends to the surface of the sand when the tide goes out and disappears below the surface whenever the tide comes in. This is more than reaction to stimuli, for the little worms manifest the same periodicity when transferred to a tideless aquarium, and continue doing so for a week or more. But we dare not use any psychological word like memory; what happens is due to a racial bodily enregistration. There is a hereditary rhythmic reactivity to periodic changes in the gravitational conditions, but the awakening of the reaction is probably helped by the changes in the amount of water and light. In a dark aquarium the rhythm disappears quickly. It is probable that racially established rhythms correlated with external periodicities play a part in animal behaviour greater than has been yet recognised, especially in regard to seasonal activities. It is probable that something of the same rhythmicity of impulse is expressed in the restlessness of migrant birds when the time comes for their journey, and at this relatively high level there

is likely to be a psychical factor that actually counts. On the tentative or experimental side, room must be left for novel answers-back to the external periodicities, such as those of the seasons, and for novel expressions of the internally rhythmic impulses.

(VII) **TROPISMS.**—The next lower grade, where the psychical aspect fades still farther, is that of obligatory movements—tropisms. By a tropism is meant an engrained constitutional obligation to adjust the body relatively to the direction of the incident stimulus so that the two sides—it may be the two eyes, ears, nostrils, antennæ, and so forth—are equally stimulated. It is not a deliberate balancing; it is an automatic means of securing physiological equilibrium. When young eels or elvers are making their way up a river, they automatically adjust themselves so that both sides of their body are equally affected by the pressure of the stream. And this tropism is sufficient to account for a great part of their apparently determined swimming against the current and straight ahead, even in rapids. What happens in an eddy we do not know.

When a moth flies past a candle it has one eye much more illumined than the other, and it automatically adjusts its body so that equilibrium of stimulus is attained. It bends round so that the two eyes are equally illumined, and if it continues flying quickly in the same direction, it must fly into the flame. If it is flying slowly, the reaction against great heat may prove stronger than the tropism in relation to light. Or if the moth turns *outwards* at the critical moment, both eyes thus becoming equally unillumined, then it will be safe from the candle for the time being.

An interesting fact is the not infrequent reversal of tropisms when a certain limit is crossed; or when there is a notable change in the environment, or in the animal's physiological condition. Some animals, like scorpions and crayfishes, that are constitutionally light-shunning (negatively heliotropic) are unable to keep away from an unusually bright light. The little crustaceans called Gammarids, that are common in brooks, are constitutionally light-shunning and given to hiding under stones; but if a few drops of acid be added to the water of the aquarium in which they are living, they become positively heliotropic! Some caterpillars are constitutionally wound-up to climb higher and higher on their food-plant (negatively geotropic), but when they reach full size and their physiological state changes, their "forced movement" or tropism reverses, and they become as bent on going down as they previously were on climbing up. It is also the case that a tropism may be interrupted by another tropism, or by individual initiative. The obligatory character of tropisms must not be exaggerated, but in the ordinary routine of the animal's life it is just the obligatoriness that makes them so profitable. In ninety-nine cases out of a hundred they work

well, and even in subtle cases where rapidity counts for much, as when the male mosquito, automatically adjusting his antennæ and body like a living gyroscope, is able quickly to find the female when she utters her shrill note, which is not to be confused with the buzzing common to both sexes.

Behaviour of Newly Hatched Loggerhead Turtle.—This has been carefully studied by Howard and Parker, and may be considered by itself, since it shows something a little different from ordinary tropisms. Suddenly ushered into a new world, the little creature hurries from its cradle in the sand to its future home in the sea. It is constitutionally bound to go down a slope rather than up (though it may climb if necessary), and it seems to be more influenced by blue than by other colours—two inborn preferences that may help it seawards—but careful experiment shows that its life-saving reaction is to move away from the more blocked and interrupted horizon and towards that which is open and free. It is normally forced to go right, though the experimenter can force it to go wrong.

"The Dirigible Dog."—A well-known American inventor, Mr. John Hays Hammond, made a very interesting light-driven machine that is called "a dirigible dog".

It moves on three wheels, two in front, which are geared to an internal electric driving motor, and the third at the back, which is the steering-wheel. On the very front are two 5-inch condensing lenses, which appear much like large eyes.

When these receive strong light-rays from an external source they influence two cells composed of the element selenium, which is remarkably sensitive to the effect of light. These selenium cells control electro-magnetic switches which, in an intricate way, regulate the current to the driving motor and also bring about the turning of the steering-wheel. If a portable electric light, such as a hand-torch, be held in front of the machine the queer contraption immediately begins to move towards the light, and will follow it round the room at a speed of about three feet a second.

It is like a dog following a rabbit. If the electric torch light is switched off the mechanical dog stops; or if the torch be quickly moved to some distance the mechanism stops, like a dog that has lost the scent. If the light be switched on again, or brought nearer, the machine begins once more to move; if the light be all to one side the machine moves to that side, and the turning will be such as to bring the shaded selenium cell into the light.

The principle of the machine has been used in connection with a dirigible torpedo, and it perhaps throws some light on the turning of the moth into the candle, for the moth seems to be automatically seeking to get both its eyes equally illumined. At the same time we

must remember that this "dirigible dog with the selenium eyes" is very far away from the real dog we know. When we compare an animal to a machine, we are apt to be more wrong than right. The animal may be a machine, but it is a self-stoking, self-repairing, self-regulating, self-preservative machine. Mr. Hammond's clever machine has a human idea inside it, but it was put there by an outside mind; whereas the dog has a mind of its own. The strictly mechanistic view of life can never get beyond such Frankenstein devices.

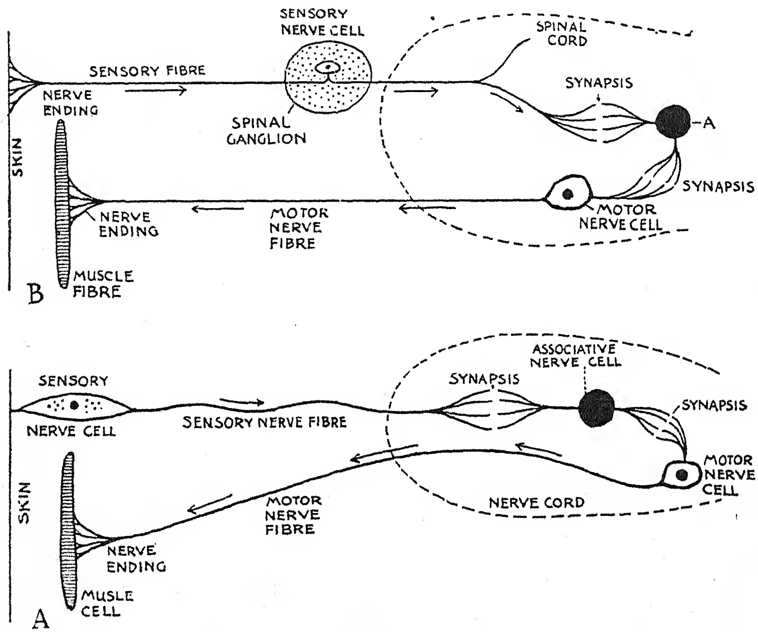


FIG. 91.

Diagrams of Reflex Action, (A) in an Invertebrate, and (B) in a Vertebrate. Modified, with permission, from Bayliss.

(VIII) **REFLEXES.**—At a slightly lower level are reflex actions. These, like instincts, depend on a pre-established neuro-muscular chain, with a varying number of links, though typically with four. As we have explained in the section on the nervous system, these typical four are: (1) the sensory neurons (*S*), (2) the associative or communicating neurons (*A*), (3) the motor neurons (*M*), and (4) the effector (*E*) muscle-cells which contract, or the gland-cells which secrete. We need not repeat the familiar story; but a distinction must be drawn between simple and compound reflex actions. When a sea-anemone closes its tentacles on one's finger, that is a simple reflex action, involving only two links—the superficial

neurons, at once sensory and motor, and the muscle-cells. But when the nestling bird opens its mouth at the touch of the food in its mother's bill, and then proceeds to swallow, this is a compound reflex action. In this typical case there are four links in the chain: (1) the sensory neurons with nerve-endings in the bill; (2) the associative neurons, in the medulla of the brain in this particular case, but oftener in the spinal cord; (3) the motor neurons in the medulla, whose fibres pass to the muscles (4) that open the mouth. More than that, however; for the opening reflex (*A*) pulls the trigger of the gripping reflex (*B*), and that in turn of the swallowing reflex (*C*), and so on it goes. Recalling *S* for sensory, *A* for associative, *M* for motor, and *E* for effector, *S–A–M–E* leads to s–a–m–e, and that to *s–a–m–e*.

The question rises here whether psychical activity has anything to do with reflexes, or is this a level at which it is entirely unnecessary to complicate description by dragging in "latent mentality" and other factors?—terms which are so apt to degenerate into verbal abstractions without any factual content, as "natural selection" has often done, and "heredity" and "variation" as well. The point is whether reflex actions can be studied whole, without any reference to the psychical side. Our answer is again a cautious negative, cautious because the physiological description here goes such a long way towards being complete in itself.

It must be noted that reflex actions are not absolutely inevitable. In certain cases the natural response—organically prepared for—can be inhibited, not merely in the human fugitive who suppresses a betraying cough or sneeze, but in the higher instances of "feigning death", as in the fox, where there may be a suppression of the natural reaction to a blow or a kick. The partly engrained, partly habituated suppression of a natural reaction in pointer dogs is well known, and the habituated control of reflexes is a common feature in training animals. Now the intervention of *control* in a physiological sequence is one of the surest signs of "mind".

Another consideration is whether it is possible to picture the evolution of reflex actions, without allowing for some variable degree of awareness and controlled testing on the part of the individual animal, and this throughout the generations during which the increased neuro-muscular differentiation and integration took organismal grip.

Let us state our position again: if it be granted that a germinal variation may express itself in structural improvements in the body, including the nervous system, there is no particular difficulty in imagining the origin of reflex arcs and actions. When the rapidity and precision of the response is of survival value, the racial establishment of an improved reflex linkage is not difficult to understand. Yet the problem is perhaps unnecessarily obscured by excluding

the operation of some degree of mental awareness which prompts the animal to put its inborn gifts to the test, especially when there is any novelty in the circumstances. Instead of looking for "mind" in the *origin* of the reflex, it may be shrewder to look for it in the testing of the hereditary equipment. If one may say so, the organism *plays its hereditary cards*. This point of view is justified, we think, by the familiar cases where animals in the course of their lifetime, and sometimes in the course of brief experiments, are able to improve upon their hereditary equipment by establishing novel reflexes on the basis of profitable associations.

Some of the simplest reflexes are very instructive in this connection. In sea-anemones there is no central nervous system, nothing more than a network of nerve-cells. Sensory neurons on a tentacle are stimulated by the touch of a fragment of flesh; the nerve impulse passes to a deeper motor neuron and thence to the muscle, the result being that the tentacle curves round the food and bends in towards the mouth. In many cases it passes on the booty to another tentacle, which continues the transport. This is a very simple reflex action, and it suffices for a considerable part of the sea-anemone's everyday life. But deeper scrutiny shows that the behaviour of sea-anemones is not so simple as it appears at first sight. Unpalatable fragments are often refused; sometimes they are positively rejected. In some cases when the sea-anemone is fed with crab's flesh and filter-paper in rapid succession, it soon comes to reject the unprofitable. In two to five days a particular tentacle, as Fleure and Walton showed, will refuse to grip the filter-paper. Yet inexperienced adjacent tentacles fell into the trap, though only once or twice. The profiting by experience was somehow transferred by the network of nerve-cells to neighbouring tentacles. Perhaps there is here a glimmering of awareness, feeble because the nervous system is so diffuse. Prof. G. H. Parker cheated the tentacles of one side of an anemone till they would not be cheated any more, but he found that those on the other side were quite liable to be deceived by faked food. Our view is that most sea-anemones get along very well without "mind", in virtue of their inborn and acquired neuromuscular linkages; and yet sometimes there is in the background a hint of an inner awareness that enables the animal to use its reflexes in a somewhat new and more unified way. Thus the beautiful Anthea allows a spider-crab to shelter between its base and the rock, and stretches down one of its long tentacles to grip the booty that the crustacean has lugged home to its retreat. It is too soon to offer an argument; but it appears to us very difficult to account for the details of the much-studied commensalism or mutually beneficial partnership between sea-anemones and hermit-crabs without crediting both parties with the stirrings of mind.

Not far from the level of automatised reflex actions, but with

distinctly experimental, not engrained, character, we would include an exceedingly interesting kind of tentative behaviour, which might, perhaps, be called experimenting below the level of intelligence. It is well illustrated by the way in which some individual starfishes, of the common *Asterias rubens* species, will tackle small sea-urchins and disarm them by wrenching off the scores of snapping blades or pedicellariæ. This remarkable operation is not rewarded until it is completed; it is far from being on the line of least resistance; it is strangely circuitous, for the starfish uses one arm after another; it is an individual activity, not often observed; and it is exhibited by an animal which has no nerve-ganglia in the ordinary sense. The starfish's nervous system consists of a pentagonal ring of simple neurons around the mouth, a strand of the same up each arm, and a loose network of similar cells in various parts of the body, for the most part not sunk in below the surface of the epidermis. The same puzzle occurs when starfishes "learn" to right themselves more and more rapidly when they are turned upside down, or "learn" to escape from staples and curved pegs that bind them down. It seems very difficult to think of such cases as illustrating purely physiological reaction and enregistration.

CONDITIONED REFLEXES.—The appearance of a translation of Prof. I. P. Pavlov's *Conditioned Reflexes* has made available a mass of experimental data, hitherto almost unobtainable by students outside Russia, in the field which that great physiologist has made his own. Certainly, Pavlov was not the first to see how artificial was the boundary which separated those activities of the nervous system which were regarded as falling within the province of physiology from those higher faculties which were approached in a different spirit and with the terms and methods of psychology; but he was the first to plan and carry out a campaign for advancing the frontier of physiology in this direction.

The simple reflexes, which Pavlov calls "unconditioned", are common to all normal members of a species; they do not have to be learned, but are inborn. If a man is sitting with one leg over the other and the foot swinging freely, a sharp tap below the knee-cap will cause the foot to jerk upwards as the leg straightens. This is one of the simplest reflexes; it does not require the intervention of the brain; the nervous impulse travels up a sensory nerve-fibre from the "receptor" in the skin to the spinal cord, along a short connective link within the cord, and down another fibre, a motor, to the muscles which cause the leg to straighten. Normally, of course, a message also goes to the brain to report the occurrence; but the brain does not enter into this simple "reflex arc". By an effort of the will, however, we can, if forewarned, prevent the straightening of the leg and suppress the reflex.

Another example of an unconditioned reflex is the secretion of saliva which follows the introduction of food into the mouth; this is a reflex not easily suppressed by voluntary effort, perhaps, but suppressed by the greater claims of a stronger stimulus, such as sudden pain, or by emotional disturbance, such as fear; which is the physiological basis of the ordeal by chewing rice, used for the conviction of malefactors in the East. But what are we to say of the secretion of saliva which may take place when we merely smell a savoury dish, or see someone eating a lemon, or—subtler still—when we hear the gong sounded for dinner? These are cases of what Pavlov calls "conditioned" reflexes. They are not common to all members of the species, for a man who has never tasted lemon can whistle unconcernedly while his neighbour sucks one; they are not inborn, for the sound of the gong means nothing to the child. They are, none the less, reflexes, and behave somewhat like simpler reflexes in their relation to the higher activities of the brain; but they are learned or acquired by each individual in his own experience. We may note that such conditioned reflexes are always based upon inborn reflexes; the response is the old one, though the stimulus is subtler than before—the aroma or the mere sight or mention or thought of food instead of its physical presence in contact with the receptor organs of the mouth.

This salivary reflex is the one which Prof. Pavlov and his colleagues have found most useful, since it is possible to estimate the efficiency of the reflex by measuring the amount of saliva secreted. Within a specially-built laboratory at Petrograd, in which disturbing factors were reduced to a minimum, they taught dogs to associate the giving of food with some other accompanying stimulus—a sound, a flash of light, an odour, or a touch—until a conditioned reflex was established and the "irrelevant" stimulus alone was able to cause a secretion of saliva. It would lead us too far to consider the experiments in detail, or the light which they cast on the processes of learning and unlearning, on the behaviour of animals generally and the functions of the brain. For these the reader must be referred to Prof. Pavlov's great book, or to such a summary as that given in Prof. Lovatt Evans's *Recent Advances in Physiology*.

(IX) **REACTIONS IN PROTOZOA.**—Descending to the level of unicellular organisms we find a number of established reactions, analogous to reflex actions; but it is desirable to keep that precise term for animals with a linkage of receptor-, motor-, and effector-cells. We are referring now to the fixed reactions that many Protozoa exhibit in response to diverse environmental stimuli. Their establishment may simply be the outcome of the selection of the relatively fitter responses. Thus the Slipper Animalcule (Paramœcium), coming within the sphere of influence of some detrimental stimulus, reverses

its cilia, backs away, turns slightly on its own axis, and then swims ahead again. If it encounter the obnoxious stimulus a second time, it repeats the process. This is the established reaction of the Slipper Animalcule—the answer it gives to almost every question; and in most cases it is very effective.

In the behaviour of many Protozoa a given stimulus is followed by a reaction which seems to depend on (*a*) the racial history, (*b*) the specific metabolism of the animal, and (*c*) the individual experience.

Thus in response to a particular excitation there may be protrusion of an unusual form of pseudopodium, such as the delicate, almost Radiolarian-like processes radiated out from the body of an Amœba when it is suspended in a large drop of water free from contact with a surface. Perhaps the same kind of novel reaction is seen among the cells of an embryo when they have been disordered, or by phagocytes in the presence of novel stimuli.

(X) TRIAL AND ERROR IN PROTOZOA.—Yet even at this unicellular level there is something different—namely, a "trial and error" testing of possibilities, the analogue of which may be recognised among many-celled animals at various levels. A good example of very simple "trial and error" procedure is afforded by the Trumpet Animalcule, Stentor, a large ciliated Infusorian that attaches itself by its narrow end to water-weed in marshy pools. It makes a temporary mucus-like tube that invests the lower half of the body, and into this it can retract itself. When Jennings allowed a shower of microscopic carmine particles to sink upon the Stentor, he observed that it may bend to one side, twisting on its stalk. This is answer one. But if the shower of particles is kept on, the movement of cilia round about the upper end is suddenly reversed, and the water is driven away from the mouth. The Stentor may repeat this two or three times, and this is answer two. But if the dust continues to fall the animal contracts into its tube and suspends activity. After half a minute or so it re-expands, but contracts again if the dust-shower continues. This retreat may be resorted to many times, and after each contraction the Stentor stays a little longer in its tube than it did at first. This is answer three. Finally, if no improvement in circumstances rewards Stentor's trials, it breaks away from its moorings and leaves its tube. This is answer four. We see, then, that the animal tries a series of reactions until by one of them it finds a way out of its difficulties. "The phenomena", Jennings writes, "are thus similar to those shown in the 'learning' of higher organisms, save that the modifications depend upon less complex relations and last a shorter time."

(XI) TENTATIVE BEHAVIOUR AMONG PROTOZOA.—But even at this low-lying level of animal activity there is the sugges-

tion of tentative and spontaneity, as is well illustrated by the account given by Jennings of the Amœba's behaviour in pursuit of a smaller one. The larger individual *A*, followed the smaller *a*, overtook it and engulfed it. But *a* escaped through a weak spot in its pursuer's protoplasm and glided away. Whereupon *A* turned on its course, and caught *a* for the second time. A second escape followed, and no recapture was effected. In cases like this there is a purposiveness in the behaviour which cannot be described in purely physiological terms. Even in the simplest forms of behaviour there is an indication that the organism is MIND-body as well as BODY-mind. When one watches a common Infusorian threading its way among the tangle of Algoid filaments and the like under the microscope, one may hesitate to use a word like "exploring", but is it possible to be satisfied with "irritability"? The Infusorian is in part reacting, like a dog hunting amidst the brushwood, to the diverse stimuli of its environment, but it is at the same time obeying the fundamental urge of hunger and self-assertiveness. If it were the size of a shark, and we were bathing in its vicinity, would we doubt its purposiveness?

GENERAL VIEW.—Our survey suggests that there are two main trends of behaviour: on the one hand, experimenting, initiatives, tentatives; on the other hand, answering back from an inborn or acquired repertory of reaction-capacities. Both modes of behaviour have their advantages and disadvantages; the perfecting of the second often makes an advance of the first more feasible, yet the very perfection of the instinctive may remove the spur to intelligence.

Beginning at the base, there are on the initiative side "trial and error" methods, pre-intelligent efforts, tentative experiments, associative learning, intelligent behaviour, and, in man, rational activities. Similarly, beginning at the base, there are on the enregistered side established reactions, reflexes, tropisms, rhythms, instinctive behaviour, pre-intelligent enregistration, habituation of intelligent actions, and subconscious cerebration.

Fig. 92 is an attempt to express the fact that the various forms of animal behaviour are on different levels of complexity; but it has, perhaps, the disadvantage of suggesting at first glance that instinctive behaviour, for instance, leads on to intelligent behaviour, whereas we hold that these two common modes of behaviour are on different lines of evolution. We have sought to get over the difficulty by using many separate branches.

Behind the diagram there is a twofold theory: (1) that as we ascend the series of animal activities it becomes increasingly possible and necessary to recognise a mental or psychical side, indicated by the dotted line on the concavity of the curve, the physiological accompaniment being indicated by the continuous convex lines;

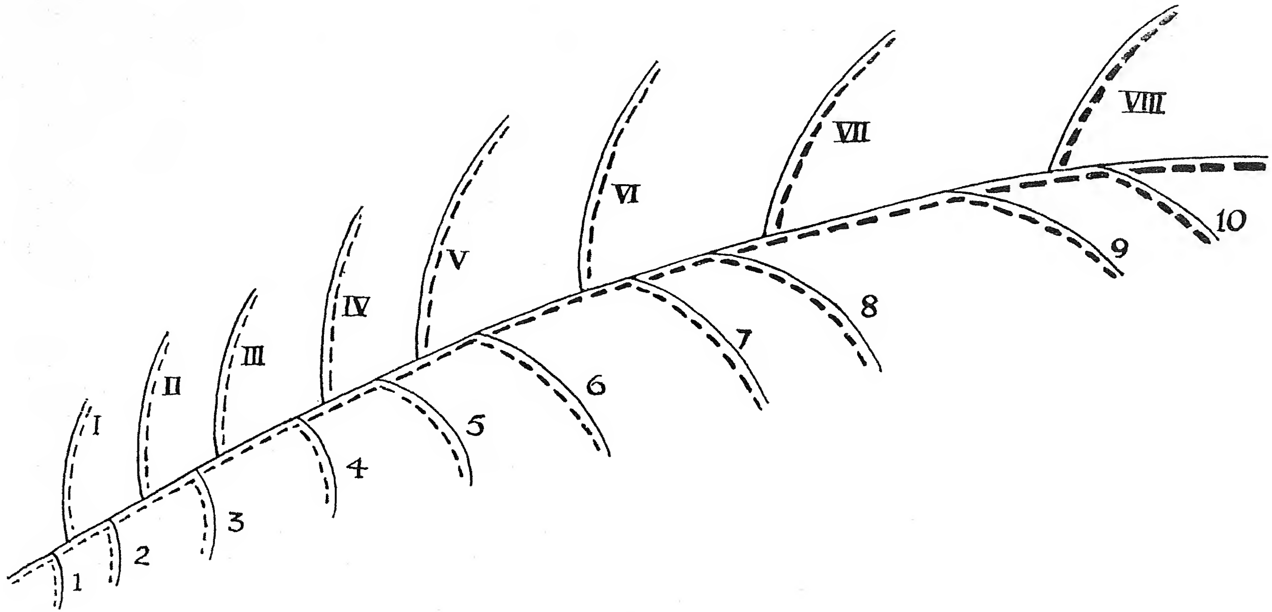


FIG. 92.

Diagram of Various Modes of Animal Behaviour. The upper lines indicate initiative and experimental activities; the lower lines indicate engrained or hereditary or habituated activities. The dotted line represents the psychical or subjective aspect; the continuous line indicates the neural or objective aspect. As we ascend the series the psychical aspect becomes more and more obvious. I, Very simple actions; II, simple tentatives; III, trial and error experiments; IV, V, VI, experiments, experiential learning, and associative learning; VII, intelligent behaviour; VIII, rational conduct, confined to man. 1, Simple reactions; 2, fixed reactions; 3, simple reflexes; 4, 5, 6, more complex reflex actions, tropisms, and enregistered rhythms; 7, 8, simple instincts and chain instincts; 9, habituated intelligent behaviour; 10, unconscious cerebration.

and (2) that animal behaviour is either predominantly *reactive* (on the lower side) or predominantly *initiative* (on the upper side). In other words, the behaviour may be in the main an expression of what is hereditarily enregistered, or in the main an expression of new tentatives and experiments.

A corollary that the diagram also expresses is the more and more manifest emergence of the mental aspect as we ascend the series. This is expressed by a thickening of the dotted line on the main stem, which is to be thought of as the general stream of life both ontogenetic and phylogenetic. Primarily the axis of our "feather" indicates the phyletic line of organismal advance from Protozoon to polyp, from polyp to worm, from worm to Arthropod and to Vertebrate; it being always clearly understood that the higher animals, such as horse and dog (and indeed man also) have reflexes, tropisms, and instincts as well as a predominance of intelligent behaviour. But without any confusion of thought the axis of our feather may also represent the individual development, from embryo to newborn creature, and thence through youth onwards. Again obviously, although there is a stage when only reflexes are discernible, these are not displaced when intelligence begins to assert itself.

Conveniently, moreover, the alteration in the thickness of the dotted line *on the branches* might also indicate, did we know enough, the waxing of the psychical aspect in initiative, tentative, or experimental behaviour, and its waning in behaviour that is the outcome of enregistration or the engraining of reactions. Thus we might indicate part of the branching enlarged to show this alteration.

Before summing up, we must emphasise the point that the survey we have taken is concerned only with that part of the psychic life of animals that may be thought of as *directly underlying* particular doings. But that is far from exhausting the mental possibilities; for even thus there is the store of sense-impressions, the accumulation of experience, the ebb and flow of feeling—sometimes rising into emotions, such as affection and anger. Account must be taken of each of these, for the enjoyment that many animals seem to display is a fact of observation, not merely at first sight to the unsophisticated field-naturalist, but after the critical scrutiny of veteran experts in comparative psychology. Thus "enjoyment" is to Lloyd Morgan one of the criteria indicative of the pervasive psychical aspect of animal behaviour, and as distinctive as controlling guidance, often with its hints of inference.

Another inquiry that should be attempted is the grouping of the springs of behaviour—the internal stimuli that lead to actions. On the physiological side they are states of dissatisfaction, restlessnesses, appetites, and so on; on the psychological side they are impulses, desires, purposes, and the like. The problem is to find an orderly grouping.

CONCLUSIONS

1. By "mind in animals" we mean whatever in them corresponds in any degree to our own inner life of thinking, feeling, and purposing; but we must be prepared to find that what is a powerful stream in ourselves is a very slender rill in many an animal.

2. The inner or psychical life cannot be reduced to a lower common denominator of nervous impulses and the like. The psychological cannot be expressed in terms of the physiological. Mental activity cannot be explained in terms of matter and energy. To mention only one reason: we require mental activity to realise matter and energy at all, before and after we investigate them.

3. No thinker has attained to clearness in regard to what is called, badly perhaps, the relation of "Body" and "Mind". We say "badly perhaps" because that way of putting the question commits one to the theory that "Body" and "Mind" can be thought of as separate realities or entities. Perhaps they are separable, as many believe, but this should not be assumed at the beginning of the inquiry. Some thinkers believe that the Mind uses the Body as its instrument, as a musician his violin. To others it seems that *mental* and bodily, *psychical* and physical, *subjective* and objective, are two aspects of one activity which we call Life—just like the *concave* or *inner* and the convex or outer surfaces of a dome. And there are other theories. But in any case the certainty is that these *are* two sides of the behaviour of man and of higher animals, and that neither can be ignored. Sometimes the physiological or bodily side is more prominent, and we say "*Bio*psychosis" or Body-mind. At another time the psychological or mental side is more dominant, and we say "*Psycho*biosis" or Mind-body.

4. Animals seldom show more cleverness than is demanded of them by the conditions of their life; and if frequently recurring difficulties can be adequately met by some inborn predisposition of the body, as when elvers swim straight upstream, or by some ready-made or instinctive equipment that does not need any individual apprenticeship or learning, there is not likely to be much (if any) evidence of intelligence on these occasions.

5. In many cases it seems likely that the psychological side of the animal's life does not count for very much in the ordinary behaviour. That is to say, what the creature does may be sufficiently accounted for by what has been racially enregistered in its Body-mind, or, as some would prefer to say, in its BODY. As Spinoza warned us, we should beware of being dogmatic in regard to what the body, as body, may not be able to do. In such cases we must try to avoid two extremes. We must not think of a minute Mind, which might be called a "menticule", sitting in the organism out

of employment, like an artist without a commission, because the body is sufficient unto itself. We must rather think of the creature as running according to an engrained bodily rule, and running so automatically that the mental side of its behaviour is not in any high degree activated.

Along with the finely integrated nervous system of higher animals there is a corresponding integration of the inner life, helped by memory and perceived purpose; and the result is an adumbration of what in ourselves we call "self" or personality. In the lower reaches of the animal kingdom there is probably no such psychical integration, no unified and unifying mind, but only the ever-flowing, though often slender, psychic rill that probably accompanies all life. To ignore this altogether would be the other extreme, that of reducing the animal to an automatic machine. That is to say dogmatically that mind does not count. But we should note that while the mental aspect may not be needed to guide behaviour by forming images and inferences, it may be an indispensable factor in the unifying of the life. It may be the literal *esprit de corps*. Moreover, feeling is a mental activity as truly as inference is.

6. In describing animal behaviour we must not be too generous, reading the man into the beast, and making every creature a Brer Rabbit. On the other hand, we must not be too stingy, trying to make out that the animal is no more than an automatic machine, or never more than a big bundle of reflex actions. We must follow what is sometimes called the "Lloyd Morgan principle"—that in describing any particular case we must not assume higher mental qualities than are necessary for a satisfactory description. In so doing we may do the animal an injustice; for we know that in our own case the simplest explanation or description is not always the true one. But it is safer to err on the side of scientific parsimony than on the side of credulous generosity. Yet again, because we can describe without using psychological terms a particular action like drawing our finger back from a hot coal, or like the earthworm jerking itself back into its hole on the approach of a thrush, it would be unwarrantable to conclude from this that the organism has no mind. A particular piece of behaviour may be apsychic; and yet the mental aspect of feeling, of desire, of memory, of imaging, may count for much in the life of the creature as a whole.

7. Another caution has to do with cases where an animal goes through an instinctive routine in a wooden sort of way and in circumstances which make the performance futile, or when it fails to adjust itself to a slight change in the circumstances, as when the Procession Caterpillars go round and round in a circle, or when a pigeon fails to retrieve its eggs which have been removed from the nest to a distance of two inches. On seeing such exhibitions we must not think of the animal as "unutterably stupid"; we must remember

that the piece of behaviour in question has been relegated, so to speak, into the field of the instinctive, and cannot suddenly be brought into the focus of intelligence.

8. Instinctive behaviour, as in ants and bees, goes like clockwork, and in many cases it is only occasionally that it becomes, say in a crisis, original and intelligent. But we are not bound to suppose that the racial establishment of this instinct was effected entirely without intelligence. Let us suppose that an animal finds itself endowed with a new impulse, perhaps the outcome of a germinal variation in that part of the inheritance which concerns the nervous system; it may proceed to test this novelty in an intelligent way. If it is a fatal new departure, that will be the end of it; if it is a very advantageous new departure, it may have come to stay. It will be added to the racial treasure-house. Even if the novelty is not in itself big enough to be of "survival value" in the struggle for existence, it may be linked to some other character that is of vital importance, and may be carried in the wake of the well-established character until it is strong enough to be itself sifted by Natural Selection.

There is no possibility, so far as we can see, of going back to the old theory that instincts result from "lapsed intelligence", or, to put it in another way, that instinctive behaviour was in previous generations intelligently controlled behaviour. The facts do not point in that direction. One must remember, for instance, that some pieces of instinctive behaviour are manifested only once in a lifetime, and no one can make even an individual habit of what is done only once. Moreover, there is great difficulty in substantiating, even in a single instance, the theory that an individual habituation can be entailed on subsequent generations. But it is quite legitimate to emphasise the importance of the individual organism's intelligent testing of variations in its inheritance. It may play the new cards in its hereditary hand, and it may play them well or ill!

9. If Reason be taken to mean, as is generally allowed, working or experimenting with general ideas or concepts, and if rational behaviour means behaviour which has conceptual inference as its mental correlate, then, so far as we know, animals have not Reason. This is Man's prerogative, occasionally used. The behaviour of animals sometimes gives evidence of reasoning, but at an intelligent, not at a rational, level. That is to say, the mental correlate is perceptual inference, putting two and two together, making a judgment, to some extent understanding the situation. If some critic says, "*I* call this reason", all that can be replied is that the scientific usage of these terms should be observed. It is not for easygoing amateurs to re-edit the scientific dictionary.

10. Evidence of intelligence is clear in the behaviour of apes and monkeys, cats and dogs, horses and elephants, rooks and parrots,

and so on. But one must not take every case at its face value. Training by man often results in an appearance of intelligence which is not there. A clever device may be the outcome of random trying and of eliminating useless movements without even picture-logic. An animal, like a man, may take intelligent advantage of what is fortuitously discovered, as is probably the case when the Greek eagle lets the Greek tortoise fall from a height so that the carapace is broken. In certain ways the highest intelligence among animals is exhibited by those that become man's responsible partners, like shepherd dogs, horses, and elephants; but allowance has to be made for direct training. It must be granted that there may be profiting by experience below the level of intelligence; thus even headless earthworms, and naturally ganglionless starfishes, can *learn*.

11. A large part of animal behaviour is *instinctive*, the outcome of an inborn, ready-made power of doing apparently clever things. It does not require to be learned, though it may be perfected by practice; it is shared almost equally by all members of the species of the same sex: it has reference to particular conditions of vital importance or of frequent recurrence. Physiologically regarded, instinctive behaviour is like a chain of reflexes; but in some cases, at least, it seems necessary to suppose that it is suffused with an awareness that rises above mere sensitiveness to stimuli, and backed by an endeavour that is more than generalised vital impulse. Instinct is seen at its highest and purest in ants and bees; it is subtly mingled with intelligence in birds; it wanes before intelligence in the higher mammals.

12. It is a common error to say that man shows intelligence, while animals show instinct. Man shows some instinctive behaviour, as well as much intelligent behaviour, and an occasional flavour of rational conduct; animals often show both instinctive and intelligent behaviour, but some show little more than reflex actions. Man has few clear-cut instincts; that term is often applied too loosely to inborn predispositions and urges, or to the general promptings of the Primary Unconscious.

13. It is a mistake to regard instinct as a low form of intelligence, or as the outcome of automatised intelligence. Instinctive behaviour and intelligent behaviour are on diverging lines of evolution.

14. There seem to have been two main trends of advance in the evolution of animal behaviour. On the one hand, there is the power of fresh adjustment, of making little experiments or tentatives. This is the line of individual initiative, and it has its climax in sheer intelligence. On the other hand, there is the capacity for enregistering profitable modes of behaviour, so that they become parts of the inheritance, requiring no more than a liberating stimulus for their activation. In both cases there is inherited capacity; but among

"big-brained" types, the inheritance is mainly the free, nimble, educable, intelligent MIND-body increasingly dominating mere BODY-mind, while among "little-brained" types the inheritance is mainly a stereotyped series of reactions—of BODY-mind with very little of mind in it.

15. Along the line which we may call the power of initiative and experiment, there is not only intelligent behaviour (rising to rational conduct in Man); there is the tentative plasticity of some humble animals like starfishes, where the absence of any definite nerve-centres forbids the use of any term like intelligence.

16. Along the line which we may call the capacity for enregistration, there is not only instinctive behaviour (at diverse levels); there are obligatory movements or tropisms, as when the elvers swim persistently upstream; there are engrained rhythms, as when the Convoluta worms come to the surface of the sand when the tide goes out, and retreat again at the first splash of the flowing wave; there are reflex actions, simple and complex, as when the earthworm jerks back into its burrow, or the nestling opens its mouth and swallows when its beak is touched by the food which the but dimly sensed parent brings.

17. These two lines of animal behaviour have their respective advantages and disadvantages. Thus what is enregistered is ready made, and it is usually quick and sure. Yet it is non-plastic and often wooden. The power of initiative is plastic; it can face change, it offers alternatives, it opens the door to choice. Yet it requires apprenticeship.

18. The two lines intersect when an animal at a juncture tries its repertory of enregistered reactions until perhaps it gets an effective answer. A trial-and-error method is very common at diverse levels; and it may be either a trying of engrained capacities or a making of novel tentatives. If only one pre-established answer-back be given, and that is effective, the enregistration type of behaviour is illustrated; if the answer-back is novel, the initiative type of behaviour is illustrated; if there is a trying of one engrained reaction after another, the two lines intersect.

19. If we picture an ostrich feather held in the left hand sloping gently upwards, with the convex surface up and the concave surface down, and with one set of barbs directed upwards and the other set directed downwards, then we have a useful diagram of the diversity of animal behaviour. The upturned barbs will represent the various modes of initiative, tentative, experimental behaviour, culminating in the high intelligence of horse and dog. The down-turned barbs will represent the various modes of enregistered, engrained, reflex behaviour, culminating in the marvellous instincts of ants and bees. The convex outer surface of the whole and of each part may typify the bodily, the nervous, the physiological, the objective. The

concave inner surface of the whole and of each part may typify the mental, the psychical, the psychological, the subjective.

20. It must be kept clearly in view that the mental aspect in animal life is not restricted to control of activities, image-forming, ideation and inference; it may realise itself abundantly in feelings, in concrete purposes, in music and artistry.

CONCLUSION: THE WAYS OF THE CAT

In less formal synthetic conclusion, it may be useful to pass from the general to the particular and to consider the behaviour of an animal familiar to all—the cat. In a scientific appreciation of an animal's ways, it is best to begin with the senses; and in some respects the cat is well-endowed. Gautier tells a delightful story of Madame Théophile's encounter with a green parrot. "The cat, after spending some moments in silent contemplation of the bird, decided that what she saw was a green chicken, and reasoned further that even if green, the chicken should be good to eat. As she sprang at him, the parrot cried out suddenly, "Have you had your breakfast?" The cat fell back; her thoughts were apparent: "This is not a bird; it speaks; it is a gentleman." Without failing to appreciate Gautier's story, we are scientifically bound to puncture it, since all the experimental evidence points to the conclusion that the cat is colour-blind. It can distinguish different degrees of brightness, but it lives in a grey world. Its very marked power of expanding and contracting the pupil of the eye may be correlated with the nocturnal hunting, when it is important to make the most of the scanty rays. The tactility of the vibrissæ is also an aid to walking effectively in darkness. Not much has been proved in regard to the cat's sense of smell, but it is probably acute. As to hearing, cats are able to discriminate between differences in sound, and can learn in forty-five or fifty lessons to associate a particular vocal signal with a particular reaction. Yet there is no convincing evidence that they can distinguish differences in pitch. Their auditory world is like that of a tone-deaf individual.

Awaiting further investigation is the "homing" exhibited by some cats; for experiments show that they can return from a place three miles off or so, to which they were carried under conditions excluding intimations from sight, hearing, and smell. They seem usually to take many hours to return, and this suggests that they have to make many tentatives. This probably holds for returns from long distances, for example, from Ayrshire to Fife; but no adequate experiments have been made with these "orientations from a distance", if such they are.

Another well-known capacity, that of falling on their feet, has

been more adequately studied. For it is known that a cat dropped from a height on a soft bed goes through a series of righting reflex-movements, activated partly from the eyes, but essentially from the semicircular canals of the ears. As to the cat's strictly instinctive behaviour, it extends from simple inborn activities like purring to concatenations like those of maternal routine. A good instance of instinctive behaviour is seen when the kitten chases a small moving object, and this is normally the prelude to the specialised mouse-killing instinct. In regard to the latter, it seems certain that it is likely to remain in abeyance if it is not activated before the third month. The trigger-pulling normally occurs when the kitten is about two months old, and it is a remarkable awakening. All of a sudden the playful and irresponsible kitten becomes transformed into a beast of prey very much in earnest. As Prof. G. S. Gates says in her *Modern Cat: An Introduction to Comparative Psychology* (New York, 1928), "The hair bristles, the tail is erected or switched, there occurs hissing, sometimes spitting, growling, unsheathing and sheathing of the claws. Even in the first kill the kitten seizes the mouse by the head, neck, or back, in such a way that it cannot bite." If the liberative stimulus is too long deferred, the relatively mis-educated kitten may grow up more or less indifferent to mice. Cat and mouse friendships have often been recorded, in newspapers at least. A cat may nonchalantly allow a mouse to perch on its back.

Generous philofelines mix up Puss's sensory acuteness, inborn reflexes, and instinctive endowments with her genuine intelligence; and the result is a very wonderful but equally *unreal* cat. Similarly, they put the results of training down to the credit of cleverness. When Stables held his cat opposite a big map of London with the chief buildings marked by dark splashes, it used to put its paw on the British Museum or the like when the name of the site was shouted out. This was very puzzling to the onlooker, but it turned out that the cat was accustomed to catch flies on the wall, and that it took the dark splashes on the map for its accustomed booty!

Cats can be trained to open boxes, to escape from latched cages, to use their paw in getting cream out of a narrow-necked jug, to press a button, to pull a loop, to ring a bell, and so on; and the teacher's usual method is to go through the process patiently and repeatedly, and to reward success generously. In other cases, the conditioned reflex method is utilised; that is to say, a real stimulus is used to induce a natural response, but along with the real stimulus there is simultaneously associated an arbitrary signal, such as a verbal command. By and by the secondary stimulus works without the first. Thus the cat "begs" when you tell it to beg, and the food stimulus may be dispensed with.

After taking account of all the non-intelligent modes of feline behaviour, it is easier with a clear intellectual conscience to discuss

the higher levels of the cat's mind; but there is less to discuss than there seemed at first sight. From the experimental data adduced by Dr. Gates, "it seems extremely probable that the cat experiences the general bodily states of pleasure and pain, and those major emotions of fear, anger, general excitement, in a manner comparable though not identical with ours". On the ideational side, the cat does not seem to be highly evolved. For although it may sometimes show an intelligent appreciation of a critical situation, and put two and two together, controlling new action in the light of previous experience, it seems to have a very limited repertory of ideas, very little memory, and still less anticipation. "Poor Pussy!" "Good Doggie!" thus turn out to be more fully verifiable estimates than we have realised in thus addressing our domestic companions since childhood.

AUTONOMY OF LIFE AND MIND

COSMOSPHERE, BIOSPHERE, AND SOCIOSPHERE.—The simple and learned are agreed that it is useful to recognise three great orders of facts. First, there is the domain of things, the physical universe, the *Cosmosphere*. It includes the distant nebulæ, whose light takes thousands of years to reach us, and the dewdrops among the grass; it includes land and sea, mountains and plains, clouds, and precious stones; it includes the long gamut of radiant energies and the gravitational pull that one body has on another; it includes atoms and the world inside the atom. This is the cosmosphere.

Second, there is the realm of Organisms, our world of plant and animal life, the *Biosphere*. It includes the hyssop on the wall and the cedars of Lebanon, the invisible bacteria, the yeasts in the rising dough, the mushrooms and seaweeds, the mosses and ferns, and all the flowers of the field. It includes the dancing midges and the whale disporting itself with its flukes, the invisible animal germs that cause malaria and sleeping sickness as well as the huge elephant, the sea's abundant progeny and all the birds of the air. This is the biosphere; which, indeed, includes ourselves so far as animals, as Linnaeus classified us long ago.

Third, there is the kingdom of Man in his higher and truly human groupings and activities, and, throughout the history of civilisation to this day, their results in languages and literature, societies and institutions and products of mankind—the *sociosphere*. The words may be bad, but the grouping is useful—cosmosphere, biosphere, and sociosphere.

These three spheres are not indeed separate, or thoroughly separable. For the physico-chemical sphere envelops and interpenetrates the biosphere, not merely because the living creature is immersed in an environment of matter and energy, with which it traffics, but because there is a chemistry and a physics of the living body. As

Huxley said, though it was only a half-truth, the organism is a whirlpool in the rushing stream of matter and energy. There are surface-tensions and oxidations, and so forth, in the living body just as in the non-living world.

Similarly, the biosphere envelops and interpenetrates the human sphere, for man depends on plants and animals and is himself made of protoplasm. Apart and unique as man is, he is zoologically a mammal. He inherits, develops and grows, he feeds and breathes, he multiplies and dies as a mammal, though he is much more. He may allow himself to become more of a mammal than he should be, and slave to his passions. He may allow himself to be less of a mammal than he should be, if he becomes selfishly non-parental. The poet spoke of himself quaintly as being "stuccoed all over with quadrupeds", even including some reptiles; man is solidary with the rest of creation. "Yet what a piece of work is a man—in reason how like a God." It is an obviously gross exaggeration that "Mann ist was er isst" (Man is what he eats); yet food is a sociological factor. A rice-society is different from a wheat-society. The biosphere embraces the sociosphere.

INTERACTIONS OF THE THREE SPHERES.—This idea of three spheres is elementary, but it has its usefulness; so let us linger for a moment to notice that each sphere may cut into the one outside it. When coral polyps build a breakwater a thousand miles long, when beavers make a dam or cut a canal, when the grass covers the earth with a protecting garment, when the debris of the carboniferous forests turns into coal, the biosphere is influencing the cosmosphere. The hand of life upon the earth is a familiar theme. Perhaps there is exaggeration in the poet's daring hyperbole: "Thou canst not stir a flower without troubling of a star"; yet the green plants have made the atmosphere breathable.

Similarly man acts on the cosmosphere with all his geotechnics, whether it be a canal at Panama or a dam in Holland. He often takes part of the biosphere into his kingdom, sometimes for great good, as when he domesticates the dog and cultivates the wild wheat, sometimes for evil, as when he alters the balance of Nature ruthlessly or shortsightedly.

We have dwelt on the swaying inter-osculating boundaries between the three spheres because we wish to emphasise the validity of these boundaries. It is of great importance to our outlook to be clear that a living creature is more than a whirlpool, greater in a way than a star; and that a human society is more than a hive, not to speak of a herd.

ORGANISM MORE THAN MECHANISM.—What reasons are there, then, for regarding a living creature as more than a whirlpool?

In other words, how does organism transcend mechanism? The reason for making a comparison with a whirlpool, or a star, or a volcano, or a crystal, and not with a machine, is obvious—namely, that a machine is a material system put together by man's device. A machine cannot be regarded as a sample of the cosmosphere; it is an embodied human idea.

(*a*) The oyster is more than the eddy, because it has not yet been possible to give in chemical and physical terms a complete account of any vital phenomenon, far less of behaviour, development, and evolution. One may isolate a good part of a physiological event, and say: Here is a physical or chemical process in a line with what occurs in the inorganic world. At a certain stage in the contraction of muscle there is a combustion of lactic acid; at a stage in a reflex action there is a very slight rise of temperature due to a thrill passing along a nerve; at a stage after a meal, a peptic enzyme breaks up a protein into amino-acids by a process of fermentation, and so on. But we cannot make a satisfactory chemico-physical ledger of a dog's or an Amœba's vital processes for an hour—there is such baffling relatedness and regulatedness. *A fortiori*, how far off is a chemico-physical account of heredity, development, variation, struggle.

(*b*) In the second place, living creatures have distinctive qualities which are at present irreducible, such as purposiveness—a wider word than purposefulness—and the capacity for enregistering experience. A volcano does work, but not in the self-preservative way characteristic of organisms. A star commands our admiration, increasing with our knowledge; but the whirligig beetle in the pond is greater than a star in commanding its course. A river carves its bed effectively and beautifully, but who can credit a river with what we must grant to a mouse—a "present foretaste" of the pleasure or pain which a certain course of behaviour will entail? A bar of iron is never quite the same after it has once been severely jarred, but this is only a distant hint of the power that living creatures have of enregistering experience within themselves. The carnivorous plant called Venus's Flytrap, that shuts quickly on an insect, will allow itself to be duped three or four times with faked food; but after that, it is fooled no more, until it has, so to speak, forgotten. A brainless starfish, with not a single nerve-ganglion in its body, learns to right itself more and more quickly when it is laid on its back day after day for a week; and a young crayfish, which has a well-formed brain, learns with astonishing celerity to avoid a pathway that includes a mild electric shock. Organisms are not isolated from the inorganic; they subsume its laws and qualities; yet they are new systems with laws of their own.

Let us explain for a moment what is meant by calling the organism a "historic being". It has a capacity for enregistering the past. W. K.

Clifford was one of the first to state this open secret: "It is the peculiarity of living things not merely that they change under the influence of surrounding circumstances, but that any change in them is not lost, but retained and, as it were, built into the organism to serve as a foundation for future actions."

It is one of Bergson's services to have emphasised the same idea. Of the living creature he says: "Its past, in its entirety, is prolonged into its present, and abides there, actual and acting." Or again, in discussing the behaviour of the starfish, Prof. Jennings says: "The precise way in which each part shall act under the influence of the stimulus must be determined by the past history of that part; by the stimuli that have acted upon it, by the reactions which it has given, by the results which these reactions have produced (as well as by the present relations of this part to other parts), and by the immediate effects of its present action. We know as solidly as we know anything in physiology that the history of an organism does modify it and its actions—in ways not thoroughly understood, doubtless, yet none the less real." This is part of what is meant by "organic memory". Nothing is more distinctive of the organism than its compound-interest enregistration, which is true even if there is no transmission of acquired characters.

(*c*) In the third place, organisms stand apart because in their higher forms they give clear evidence of a mental aspect, which does not find distinct expression in the domain of things. We may perhaps believe that the mental aspect is potential or implicit in the inorganic, as in the diamond or the dewdrop; we may perhaps believe that the mental aspect sleeps and dreams in the plant; but what we are sure of is that many living creatures profit by experience and control their life-events. They remember what is past, they anticipate the concrete future, they enjoy the present. All is, as it were, on a great inclined plane—not more than flashes of mind in the Amœba, a slender slow-flowing rill in the jellyfish, a somnolent mind in the corals whose beauties are their dream-smiles, an instinctive mind in ants and bees whose behaviour is but dimly suffused with awareness and but vaguely backed by endeavour, an intelligent mind in many a bird and mammal, a rational mind in man—but some mind through and through. And what is true of the grades of being is true in the individual becoming, as is so familiar in the development of a child from an awakening that cannot be dated to an awareness that is hailed with parental pride, and from a foretaste of pleasure revealed in the eye to an evidently deliberate plan to enjoy. It is certain that psychosis and biosis are intimately correlated; it is probable that every organism is at once embodied mind and enminded body. In any case, the first organisms were new "wholes" or syntheses as distinguished from non-living things.

AUTONOMY NOT INCONSISTENT WITH CONTINUITY.—Care must be taken with the term "autonomy"—dangerous both in theory and practice. It is justifiable in theory when we are dealing with an order of facts which we cannot describe satisfactorily without using special formulæ or categories. When we pass from non-living things to living organisms there is an intrinsic newness; a fresh aspect of reality has emerged. But this newness must not be exaggerated into discontinuity. A living body is usually built up of thousands of coherent cells, and it may be that this cohesion of cells to form a body is a continuation of the aggregating and integrating tendencies which we recognise in electrons and protons becoming atoms, in atoms becoming molecules, in molecules becoming groups of molecules. Some of the properties of life depend on the fact that living matter is in a colloidal state, that is to say, it consists of innumerable ultra-microscopic particles suspended in a fluid phase, or droplets immersed in a jelly-like matrix, with the result that there is a very large surface on which chemical and physical changes may take place. We may think of a drop of fluid protoplasm as like a vast archipelago of islands with a correspondingly large coast-line for traffic. But it must be kept in mind that many inorganic substances, even gold, may occur in the colloidal state. Organisms are by themselves apart; but they are not alien to the cosmosphere. We must not jettison continuity of evolution in our desire to emphasise autonomy.

Much that goes on in plant or animal can be described in terms of chemistry and physics, and this mode of analysis has been richly rewarded. It may be called, with Comte, a legitimate materialism. But to say that vital activity in its wholeness can be satisfactorily described in terms of chemistry and physics is not at present an accurate statement. It is an inaccurate false simplicity. Perhaps it may be said that this is an *argumentum ad ignorantiam*; for the satisfactory mechanistic description may be forthcoming some years hence. But is this not another kind of *argumentum ad ignorantiam*? We must make our balance-sheet for the scientific firm as its affairs stand at the time; we cannot make assets out of possibilities. But perhaps it will be said that the chemistry and physics of 2030 will be as different from those of to-day as these from those of 1830. This is likely enough, but perhaps that will in part be because Science has read back into the cosmosphere the lessons learned from a study of the biosphere. But sufficient unto the day are the problems thereof, and while we are pleading for a frank and full recognition of the chemistry and physics of the living body, we are not pretending that we can arrive in this way at more than a very partial understanding of, say, our dog or horse.

MECHANISTIC AND VITALISTIC VIEWS.—In the long-

drawn-out mechanistic versus vitalistic controversy, we must not allow ourselves to be influenced in our thinking by any thought of consequences. The only scientific questions are: Is the mechanistic description of the realm of organisms adequate or inadequate? Is a vitalistic description legitimate and really needed, and, if so, in what terms?

When studying living creatures we must try to steer between an abstractional Scylla and a materialistic Charybdis. Scylla has still her many heads, of which "vital force", "entelechy", and even "élan vital" are three. Charybdis is still voracious, violently reducing to a lowest common denominator everything that she can suck into her vortex. No doubt she can reduce the living organism—say the dog—to electrons and protons, but this does not help us to understand our dog as dog. And that is what we aim at as biologists.

Is there or is there not in the dog anything besides matter, and energy, and mind? But this way of pressing the question forgets or ignores the fact that matter and energy and mind are abstracted aspects of reality. By the methods that reveal matter and energy—or electrons, protons, and radiations—nothing else at present can be disclosed. Even if we are convinced of the reality of a quite specific "vital force", we cannot demonstrate it by chemico-physical methods. If we could it would not be specific. This does not seem to be a way out.

Between the abstractional Scylla and the materialistic Charybdis, both metaphysical, is the passage called "methodological vitalism". This does not postulate any "vital force", "biotic energy", or "entelechy", yet it reacts from the attempt to coerce the organism into the framework of mechanism—grand as that framework may be, as the stars on high declare. What a methodological vitalism says is simply this: There is a chemistry and physics, a mechanics and dynamics, of the living organism; but, when they have finished their ledger, the description is biologically inadequate.

An Aberdeenshire swallow banded when full grown with a marked aluminium ring of no great weight, came back after its winter sojourn in Africa to its native land, county, parish, farmstead. Suppose we were biochemists and biophysicists knowing enough to make a ledger of all the metabolisms—chemical and physical changes—between the date of the swallow's liberation and the date of its recapture, would this make sense of the fact established? It would not, and nothing will, except a biopsychological theory of the bird as a "historical being", meaning by that a creature that carries its past engrained within it, lasting and working. But does not a comet return on its majestic curve with predictable punctuality? It does, and we feel sure that Halley's comet, last seen in 1910, will be back again in 1985; but the swallow differs from the comet in being individually adjustable, in having a measure of

indeterminism, in being free to err, and in being able to hand on its way-finding capacity as a heritage to its offspring.

It is not difficult to multiply cases where the chemico-physical description of vital activity does not in itself make sense; and this is just another way of saying that biology is autonomous. Yet this is too negative a position. We must go further and seek to define the characteristic qualities that give the organism its newness. It is not enough to tie up the puzzles of life with a label called "*x*". At all events we must first be ready to state what these puzzles are; and we must welcome their reduction to simpler terms if that is practicable.

As we have explained in the first chapter of this book, organisms have a characteristic self-preservative metabolism of proteins in a colloidal state, always changing and yet remaining for variable periods the same. Organisms are able to grow, multiply, and develop, continuing their specific organisation or individuality from generation to generation. Organisms show a purposive behaviour, a power of enregistering individual and racial experience, and a capacity for varying and evolving.

So far as we are aware, nothing happens in living creatures that is inconsistent with the laws of chemistry and physics, but new things happen—profiting by experience, the bent bow of endeavour, processes of self-regulation, self-repair, self-multiplying. This is the Autonomy of Life. So, if we speak of *the* Order of Nature, it must be more than the Order of the Cosmosphere, it must include the higher order of the Biosphere, in which new aspects of Reality have emerged that require categories of their own. George Henry Lewes used the word "emergent" as contrasted with resultant, when the new product shows more than the sum of the old properties and qualities; and this usage has been elaborated and refined by Lloyd Morgan.

An attempt must be made to avoid the fallacy of hard and fast lines in speaking of autonomy. We emphasise the autonomy of life because we wish to avoid the false simplicity of calling an animal a mechanism, yet every new synthesis implies some degree of autonomy, so we must use the term warily.

One can fancifully picture a disembodied chemist studying a world of gases; and some worlds are gaseous indeed. A star may be without solidity, we understand, and consist of electrons and protons, maimed atoms or ions, and storms of ether-waves. One can imagine the disembodied chemist coming to know much in regard to the laws of gases, and attaining to a very vivid picture of the dance of molecules and their interminable collisions. But after many Jehovan days, in which a thousand years are as one day, hydrogen and oxygen unite, in the chemist's cooling world, to form water, the first known liquid, let us suppose, with novel and surprising

properties almost, if not quite, unpredictable. Water is thus a useful illustration of an emergent, yet it is doubtful whether it is profitable to speak of the autonomy of water or of hydrology. For from our knowledge of the movements of particles in a gas we can advance some way towards an understanding of their restricted movements in the liquid state. It is a question of degree. But our point is that the living differs from the not-living *so much more* than water differs from a mixture of hydrogen and oxygen, that we should speak of the autonomy of Life.

We cannot describe the behaviour of a migratory bird in terms of protons and electrons and radiations. Even if we could, the description would not be what we wanted, for we cannot make sense of the bird's behaviour without considering it as a "historic being", as a creature that enregisters the past.

Moreover, we must not think of electrons and protons and ether-waves as being in some special way "bedrock". All that we dare say is that they are the lowest common denominators at present available for the analytic description of the physical aspects of things. Already we are beginning to hear hints that the electron may not be the last word in atomic micro-analysis. Electrons and protons seem to be the stuff out of which the worlds have been spun, but we must not be too sure that they are irreducibles, or that they are more of the nature of bedrock than, say, an animal's purposive self-preservative behaviour.

Our point is that electrons and protons and radiations are those aspects of reality which are disclosed by particular methods of scientific analysis. They are the species of fish that are caught in the sea of reality by using a particular kind of net and a particular size of mesh. But there are other sizes of mesh, and fishes may be caught without nets at all. Scientific method is not the only right of way to reality.

MIND AND BODY.—As to the autonomy of mind, it is logically a postulate. Natural Science deals with the measurable, but we cannot measure our measure. By no dialectic sleight of hand can we build up mind out of materials that mind has furnished or mirrored. By no verbal jugglery can we get the inner rill of mental life out of the stream of metabolism.

But apart from these and similar arguments, it is a large fact of Natural History that the more intimately we know animals, the more does "Mind" seem to count. And perhaps the largest fact of Organic Evolution is just the gradually growing freedom of mind, as we work upwards from simple creatures to the intelligent birds and mammals. Not merely does the mental aspect become a more prominent feature in the life of the creature, till it comes to look like a conscious control of behaviour, as we know it in ourselves;

but there is, if our interpretation is correct, a growing emancipation from the trammels of the flesh. More cautiously, keeping, though without dogmatism, to our personal monistic way of looking at things, we mean that the higher animals are increasingly MIND-bodies as distinguished from BODY-minds. Concretely, we mean that although the bird at the breeding season is profoundly swayed by the chemical messengers called "hormones" that are distributed by the blood throughout its body, strong keys unlocking doors long shut, the nightingale's lyric illustrates what we would literally, not fancifully, call an emancipation beyond the "body". We may be wrong, but we cannot get away from the conviction that the bird feels joyous, and that its joy is just as real in its own way as are its hormones in theirs. Moreover, for some birds that have a well-defined breeding and brooding "territory", such as a particular oak-tree or alder-tree, it seems, as Mr. Eliott Howard has shown, impossible to make sense of their behaviour without crediting them with an imagery of their home and a power of reviving it.

The extreme "behaviourists"—who have nevertheless done good service in showing what the body as body can do—deny that "mind" functions as an appreciable *vera causa*; but it is easy to bring forward analogical evidence to show that the animal often acts on the strength of some psychical activity, such as is implied in a memory, or a mental image, or a surge of emotion. An animal will act on the remembrance of an injury or a kindness long past. A chimpanzee will whittle a stick with its teeth till it is of a size to fit into the hollow end of a bamboo rod, thus making out of two sticks one that is long enough to reach a desired fruit lying outside the cage. Many an animal will fight to the death for its family, or expose itself to hopeless odds to shelter a young one; and a deer has even come to die at the spot where its mate was shot.

The extreme behaviourists maintain that mind, though present as an epiphenomenal by-play, does not count in animal behaviour; but the very reverse seems to us to be indicated by the animal's search for suitable environments, by such subtle life-saving devices as some forms of death-feigning in higher animals like the fox, by persistent endeavours towards a distant and often unseen goal which once brought pleasure or even joy, by cases of perceptual purposiveness such as the chimpanzee's piling one box on the top of another to the number of four, so as to reach a banana hanging from the roof out of normal reach, by the often elaborate training of the young in the art of life, as in the case of otters, by the many conventions of animal societies, and by occasional instances of intelligent co-operation with man, as in tamed elephants or in sheep-dogs. Mistakes have been made here and there in appreciating the mental aspect of animal behaviour too generously; but there is cumulative evidence in favour of the conclusion that *mind counts.*

There is no scientific test for mind; we can only argue that the description of the animal's behaviour in a particular case is not good sense if we leave "mind" out. The attempt to treat animals apsychically does not work either in theory or in practice. We do not make the most or the best of our horse or our dog on an apsychic theory, and we certainly do not understand it in all its behaviour. To suppose that mind does not count in man is an obvious absurdity, though it must be admitted that we have in the past under-appreciated such factors as hormones and the Unconscious. And if it be maintained that man is the only organism in whose behaviour mind counts, then we are making him, if we are evolutionists, a very quaint mental Melchisedek.

It is difficult to take very seriously the extreme view of man as a machine, *l'homme machine*, a machine with an intermittent safety-valve whistle, called mind, which is all sound, signifying nothing; and the extreme behaviourist view lands us in this absurdity. No doubt reflexes, tropisms, habituations, and enregistrations in the body count for much; it is part of Nature's tactics to automatise. This automatisation is justified by its everyday ready-made efficiency, and also because in many cases it leaves the higher faculties more free for initiative. No doubt the ductless or endocrinal glands, such as thyroid, suprarenal, and pituitary, count for much; but it is a gross exaggeration to speak of them as *determining* the personality. No doubt the mind sometimes suffers from being immersed in an unsound body, yet how many invalids have proved that mind may be victorious over a sea of troubles! Is man going to surrender his birthright of making his psychic MIND-body transcend his organic BODY-mind?

We are told by a physiological authority that man is an "adaptive mechanism", which has among its functions "the fabrication of thought", including, of course, the mechanistic theory. But a machine cannot have a theory that it is a machine.

In connection with the autonomy of mind we wish to say a little in regard to the repercussion of evolving mind on evolving body. We know something of the mind's influence on the body in the individual life-history, not only in everyday reactions, as when emotion thrills the whole body through the endocrinal or hormonic system, but in subtle cases, as when "her temple face is chiselled from within". But let us think of this also in regard to evolution. The individual mind—an aspect of the reality we call life—reacts continually on the individual body, and makes it possible for the organism to play more effectively the structural peculiarities in its hand of hereditary cards. This is one of the ways in which mind works as a *vera causa*, not only in individual development, but in racial evolution.

DISTINCT ORDERS OF FACT DEMAND DISTINCT FORMULATIONS.—What does all this amount to? We do not know the secret of life, but we are convinced that living creatures are more than mechanisms, and that they have qualities requiring special categories for their due description. This is the autonomy of life, and if we are to avoid false simplicities we must hold by it.

We do not know the relation of "mind" and "body", if it be a relation, but we know that there is the closest of correlations. Some would say that the mind plays on the body as the musician on his instrument, the very attractive definitely dualistic view. Others would say that mind and body are two aspects of life, as inseparable as the inner and outer surfaces of a dome, or the concave and convex aspects of a curve. As Lloyd Morgan puts it: "*All* the events which, as physiologist, I study, are connected with psychical events; and *all* events which, as psychologist, I study, are connected with physiological events." This is the monistic view, as the anti-theological Haeckel indeed named it, yet which in Lloyd Morgan's case, for instance, is not inconsistent with being a religious man and a convinced theist. But our point is simply this: that whether we are dualists or monists, we must admit that the mental aspect is as real as the bodily; and that it is so different from the metabolic or neural or protoplasmic aspect that it requires categories of its own for its description. This is *the autonomy of mind*, and to avoid false simplicities we must hold by it.

We must try in the name of science not to allow wishes to father thoughts, as they are so prone to do. What is the most accurate way of stating the facts? That is the primary question. But when we pass beyond science to a synoptic view which includes all that we have gained in our practical experience of life and mind, and all that we have gained along the pathway of feeling, we may perhaps come to this practical conclusion, that there is something wrong with our science if we are not led to think *in a big way* both of life and of mind, and of these more and more in harmony, and in progress, in which surely mind goes further of the two—whence even growing bodily old has often its compensations.

In another section we must thus say something in regard to the autonomy of Sociology; for the Kingdom of Man requires categories of its own, and human society transcends the individual as the hive transcends an individual worker-bee. Moreover, as all must allow, a human society is at a much higher power than an ant-hill or a beehive, a herd of antelopes, or a beaver village.

In short, then, to try to force the whole life of organisms into the framework of chemistry and physics is, we maintain, an illegitimate materialism, to be guarded against, and similarly to try to force the life of human society into the framework of zoology is in its way as bad, an illegitimate biologism, to be guarded against. Yet it

is often more difficult to guard against, since simple forms of social life are found in the animal world, and our human-animal life underlies and interpenetrates our social. Yet here psychology—though also of evolutionary rise from simple to higher forms—comes in to aid us: for in all our human societies, from simplest onwards, there is a psychosocial life which in higher ones becomes "the spiritual power", that of the psychic life more and more fully dominating the physical. We may trace this from its beginnings with the shaman and the medicine-man; and advance to the solitary hermitage, and thence to the associated cloister. We see how such have been characteristic, in various yet kindred forms, of each historic faith; and thus modifying, sometimes even transforming, the material life of the community, its "temporal power", to a veritable associate, and sometimes even too much an instrument, of the spiritual. Hence, too, we better understand the great historic founders, each at first with his single or few adherents, yet these increasing, and even some day dominating their peoples; at best to issues of peace, yet also at times to war. History is thus more than annals of place, work, and people, as they have developed to material wealth and temporal power. It is, above all, the record and interpretation of thought: and its greatest records are those which tell how thought deepened, not only to individual creation, but widened also to some higher conception of social life; and with this emotionally thrilled, imaginatively and symbolically conceived—and thus inspiring its community to better life, to worthy deed. How? Through arousing its folk to citizenship, their "polis" into a true Polity, even as Etho-Polity; and this giving to their work something of new energy, even to synergy; and this applied to such achievement as they imaged.

Such is the history of Athens and of Rome at their best, and hence their achievements; as from Theatre to Parthenon, to Pantheon and Forum, with all that these imply. And as the now incipient wave of evolutionary progress rises, may not our cities also in their turn awake to fuller life, and shape themselves nearer to the City of the Ideal? History thus above all turns on the evolution of individual minds and souls, and these to highest community, truest fellowship.

8. WHAT OF THE "SOUL"?—Let us end with a speculation which some will regard as a certainty that might be assumed, and others as foolishness. A survey of the world shows a *hierarchy of syntheses* —what Smuts has called a progressive sequence of "wholes". A living organism is a new synthesis compared with a crystal. An average representative of the species *Homo sapiens* is a new synthesis compared with a dog. But what if this process of successive syntheses or emergences is still continuing?—and what if in man there has been long emerging a new and essentially psychic integration—for which (despite present psychological convention) what better name

than *soul*? The personality, roughly defined, is the integration of the psychical life into an active unity; yet which in too many human beings is still but adumbrated (or sometimes dissociated), and which animals never or hardly ever reach. Animals remain individualities or sub-personalities, and are often very attractive as such. But what if there be evolving in Man a super-integrative, and so far untrammelled, soul or spirit, above the normal personality, as that is above the humdrum unawakened mind? And what if this be the element of synthesis that gives its characteristic autonomy to religion—which is ever sending out its tendrils towards the spiritual reality of the universe, and so far realising it in life? For are we not discerning in evolution, and at all its levels, both cosmic and human, and ever more widely and deeply—indeed as its supreme synthetic and emotioned aspect—the harmony of Good, True, and Beautiful? If such be the psychic macrocosm, do not we—as each a microcosm—at our best respond to its influences, and thus ourselves advance to souls awakening to sympathy with all those thinkers, poets, inspirers, and more, whom we most honour through history, who have already expressed something of this harmony? So what clearer unifying call, alike for individual development and collective evolution, than "Thitherward"?

THE PHYSIOLOGICAL AND THE PSYCHOLOGICAL

Dr. E. S. Russell, in his *Study of Living Things*, begins with the simple uncritical and unsystematised but practical understanding of life which has been acquired by mankind throughout its past, and which we individually acquire from childhood onwards; and he thence seeks to develop a scientific biology, which shall not be so far divorced from the practical understanding of living things as is the materialistic biology of the present day. For as we know ourselves as living beings, so we recognise other organisms by their activities comparable to our own; so all with a principle of individualised activity essentially identical with that of our own conscious and organic life: whereas the Cartesian treatment of living beings on the same footing as inorganic bodies splits up the science of life into a physics and psychology, and with too little regard of the latter, and yet less success with their clear reconciliation; even by vitalistic theories invoking the addition of some immaterial agency to regulate the mechanical, physical, and chemical processes to which physiology is reduced. Yet, biologically viewed, living things manifest activities of a higher functional order than can be expressed in physico-chemical terms, while psychology is needed for interpretation of behaviour: so that through the combination of these methods we must look for the development of a coherent and autonomous

science of life. He thus agrees with Dr. Haldane, and reinforces his lines of criticism and reconstruction; and rightly insists that "materialistic physiology goes to the opposite extreme from morphology: for while the morphologist studies form and structure in almost complete isolation from its environment, the physiologist merges it completely into its surroundings, and robs it of all independence". He ably continues these criticisms: yet also brings out the weaknesses of vitalistic endeavours, those of Driesch for choice. Yet passing to the frankly psychological point of view, he conceives of other living things as subjects, each an experiencing, perceiving, striving, and active individual; and reacting to its perceived world in such a way as to satisfy its own needs and desires: i.e. with its own view-point, not ours. Such behaviour may, of course, be psychical without being self-conscious. They are thus to be conceived as psycho-physical individuals, neither purely physical, nor yet with action on their bodies of any soul or entelechy, for both matter and soul are conceptual figments belonging to another philosophy.

Biological vitalism is philosophically derivable from idealism, so the biological method implies essential elements derived from the psychological conception, and rejects the materialistic philosophy completely. Development and functional adaptation are subject to laws of their own, which appear neither physical nor psychological, but functional or biological. Cuvier and Lamarck, Darwin and Roux, despite all their differences, are claimed as following this functional tradition: for biologists thus best study the living thing itself, leaving aside theories as to its ultimate nature. This functional biology starts with the individuality of the living thing and not with its material analysis; and our ultimate biological concept is not matter, nor even energy, since these are physical, but activity, and this not simply self-maintaining, but ever urging towards achievement, in self-development and race-continuance. By perception (or at simplest *reception*) life becomes individualised, and further its response implies continuance or duration of hormic impulse, and is varied to the environment as sensed. In terms of mere physico-chemical interaction these insignia of individuality are necessarily ignored. Yet the living being is not a mechanism actuated by a psyche, but modelling itself, in short, in creative evolution. The perceptive and responsive relations between organism and environment are thus an intimate psychological unity, as in our own experience, and are similarly discernible in behaviour, and thus in synthetic terms of the real life and activity of the organism with its changes of form in relation to environment, and not simply in tropisms isolated from these.

Dr. Russell next inquires how the psycho-biological method can be applied in practical research, and points out that organic response surpasses its merely mechanical and physico-chemical processes,

since there enter into it the future under the form of prospective tendency or horme, and the past under the form of retrospective bias or mneme; while the present too is regulated through elementary perception. And since responses involve the orderly activities of many organs, and thus of their many component cells, they correspond to the functions of ordinary physiological language, save that we must now ascribe to these the same elementary psychical moments—awareness, mnemic action, and regulability—which characterise the responses of the organism as a whole. A cell's or organ's function is thus not the materially determined outcome of the physico-chemical configuration, as for the materialistic philosophy; it is an activity *sui generis* of the living unity, and not completely reducible to physico-chemical processes, though dependent upon these. The analytic scope for physico-chemical research is next outlined; but the general functionings and responses are reserved to biology proper. The metabolic functions—of feeding, digestion, absorption, transport of material, storage, secretion, excretion, and respiration—render possible that of differential growth, fundamental to development and differentiation (or de-differentiation), which may be taken with multiplication by division and regeneration of lost parts. Apart from these morphogenetic functions, movement and receptivity are next considered.

Keeping as far as may be the term *functions* for activities of the parts, and *responses* for activities of the whole, these latter are grouped as self-maintenance, development, and reproduction, the fundamental hormic impulses of life, which are again expressed in terms beyond those of the simply physico-chemical level of explanation. Yet this functional method requires no recourse to any problematical interaction of the physical and the psychical (if such exist separately, save as logical blind alleys or termini of thought). It deals with the living being as a psycho-physical unity, before dissociation into its two complementary aspects. In his final chapter, the outlook for this functional biology, Dr. Russell indicates lines of attack on major problems. He repeats the rejection of the hypothesis of material determinism, and reaffirms limitation of biophysics and biochemistry to adjuncts of biology proper, and especially with regard to the material conditions of life and associated functioning in detail. He reserves for functional biology proper the study of vital phenomena in terms of functions and responses, with constant regard to the prospective and retrospective character of these activities, and in particular to the all-important fact of regulation. As examples of how this will work out in practice, he takes the main problems and theories of development and heredity; and criticises their long predominant insistence on the material aspects of the process. Stating them in terms of the functional activities, present in the fertilised ovum from the outset, there is

specialisation of function and integration. and in each species on its definite lines to definite form. Yet this process is not automatic or stereotyped, since the embryo may exhibit considerable self-regulation, and vary its development to cope with unusual or adverse circumstances. Development is so far recapitulatory: yet in early development organs are formed in advance of functioning: and as development proceeds, their full differentiation then becomes dependent upon their functioning. Of these two stages of development the mnemic theory affords a simple solution: organs originally formed in response to particular environmental stimuli may lose their dependence upon the functional stimulus, and appear in ontogeny in response to an associated stimulus, or in the absence of any stimulus at all. The mnemic theory in this way allows for a transmission of acquired characters—and affords also an explanation of recapitulation. From the functional and mnemic view-point, the essential thing in heredity is the transmission of tendencies—virtual or potential functions—and the essential thing in development is the actualisation of these.

Russell, with the unity and simplicity of his psychobiological treatment, does not apply our distinction of biopsychologic and psychobiologic; indeed, he may at first sight even disapprove it, as savouring of "dualism", or of "interaction", in the usual senses. For we may seem to be assuming a dualistic separateness as of old between mind and body, yet this with alternate interaction too. In the theory of interaction a bodily stimulus is communicated to the psychic life, which Huxley thus called mere "epiphenomenon": but we call this whole process, in both aspects, biopsychological. Conversely, when psychic impulse seems antecedent to the material response, though both are again viewed as aspects of a unified process, this we call psychobiological. The notation above employed may so far appear of a dualistic kind, but this is not its intention. Yet its employment in this form at the outset has conveniences, since the very terms biology and psychology have arisen from the apparent distinctness of their respective phenomena and processes; no one can help using their respective vocabularies; since there is as yet no adequate intermediate or unifying one.

On this notation, then, the unified character of life is maintained: albeit also with the physiological and psychological distinctness of customary thought. How is the reconciliation possible, and even satisfactory? We habitually view curved surfaces as concave or convex, witness cup and ball, egg and eggcup. Even when the form of a familiar object shows both together as with cup or spoon, it is their concavity which is important: whereas it is the unbroken, full and convex egg which we recognise and select, with little heed of eggshells emptied to concave. Again, viewed from opposite sides of the table, this curve is convex to me, but is primarily concave to

you; and vice versa, e.g. $\underset{A}{\overset{\downarrow}{\smile}}$ and $\underset{B}{\overset{\frown}{\uparrow}}$. So in union, the straight line conventionally separating biosis above from psychosis below, becomes $\overset{\downarrow}{\smile}\overset{\frown}{\uparrow}$ for Biopsychosis and Psychobiosis respectively.

Take now the example of a circle. Viewed from within, we realise its radii and diameters, its arcs and chords to any extent; and we can inscribe figures to any extent also. We have thus a legitimate and even necessary minor specialism, with its Euclidean propositions, riders, etc. Only when viewed from without, have we the concept of tangents. And as these also are a minor infinity, we may draw out an elaborate tangentography in the concrete, and also reach a lucid tangentology in the abstract! But when secants emerge from or enter our circle, our two minor specialisms are at first disturbed. Yet soon lucidly reunited; for their co-specialism, which is the full and proper geometry of the circle, now appears.

Return now to our notation. Though a straight line has no thickness, it is of its very nature to show two opposite and complemental sides, and these cannot be dissociated. For its changes to curvatures, the mathematician as such has no need for either material forces or psychic ones as explanatory. That graphs are graphs, is enough to him. But the physicist, and the physiologist also, recognises force at work; as in the mathematician's muscular contractions, movements, and pressures in drawing his curve. So equally the psychologist recognises the psychic urge, and the reasonable purpose, without which there would be no mathematician. Obviously, both view-points are necessary. So, as a convenient convention for graphic purposes, we here assign the upper portion of space on our diagrams of life, that above the median line, for the mechanistic process, the customary physiological view, with its objectivist statement and expression. And, complementally, the lower portion, below the median line, is reserved for subjectivist presentment, i.e. of the psychological aspect and view.

In this way, then, our diagram arises. In customary physiological terms, stimulus and response in the organismal world may be written in words, as:

Environment—function—organism, and Organism—function—environment; or in short as = E*fo*—O*fe*.

And correspondingly our own activites, as human (and thus social, for the individual is still folk-unit, as well as species-unit), are conveniently presented at simplest as:

Place—work—folk : Folk—work—place
Pwf : Fwp

But our human life is significant to us as psychic; and we are all

agreed that we have sense, experience, and feeling, whereby the outer world, of place, work and folk, comes into touch with us. We know that all these can and do influence each other, and our resulting conceptions of place, work, and folk develop accordingly. Yet a little reflection shows: (1) that we especially sense our environment, our *place*; and also (2) that we gain experience from our functioning, our *work*; and (3) that it is essentially from our folk, in our human relations, that our feelings have been developed. Hence our formula of the life-process conveniently begins as:

$$\frac{\mathrm{E}}{\mathrm{S}e}\ \frac{f}{ex}\ \frac{\mathrm{O}}{fg}$$

and develops to

$$\frac{\mathrm{E}\ \ \mathrm{F}\ \ \mathrm{O}}{\mathrm{S}e\ \ ex\ \ fg} : \frac{\mathrm{O}\ \ f\ \ e}{fg\ \ ex\ \ se}$$

The capital letters express that stimulus issues from Environment, and is (or may be) sensed; while response comes from Organism and this (as if) aroused by antecedent and continued Feeling. And is not the active response, the functioning on environment, often manifestly as if guided from experience?

Instincts, of course, need no such guidance; though even for these it is difficult for the evolutionist completely to exclude the long-accepted doctrine of ancestral acquirement through habit. The resulting change on environment, wrought by the organism's active functioning on environment, be this instinctively or more or less intelligently, may be appreciated by our senses (though not in all cases).

But in our first half-formula we all habitually think in the terms of the mechanistic physiologist. Our ordinary recognition of a stimulus is biopsychological, say of a fly on one's nose; while our response for its dismissal has as obviously a psychobiological character, elemental though this be. More developed illustrations may next be worked out in detail. Yet to do this, upwards from organisms at their simplest, from Amœbas and infusorians upwards, or again for man, and from *his* simplest to highest, is a long story, a vast range of evolutionary complexity. How shall we devise an orderly and graphic method available throughout? Is not this already in germ in the formula before us? Let us see.

Let us begin with our human sense, experience and feeling, considered in their simplest relations to place, work, and folk, and thus essentially as biopsychoses. Yet environment not only passively impresses sense, as may a falling water-drop; it arouses sense, to sense the environment, and so observe the rain. The young babe soon feels the mother's caress, but at three months is returning it with a smile. And so, after pleasant and painful experiences, these

react on action accordingly. Already their Biopsychosis is turning to Psychobiosis.

But these simple changes are not enough to explain activity proper; they do not reach the higher expressions which characterise mentality fully human, and which are known socially as "Conduct", individually as "Behaviour", or in external resultant as true "Activity"—always in some measure creative, since modifying environment in some significant measure.

For convenient beginning of this needed inquiry into further developments, note how the child one day reaches the level of "make-believe", and increasingly delights in it, with new and enlarging activity. The little girl's first extemporised dolly is the standard example of this; for here is the dawn of her coming womanhood; and in this we see the rudest rag-bundle transformed from sense-object to imagined child. That imagination can and does thus work on sense-material, and subjectively transmutes it, is surely the most undisputed of all psychological interpretations; so the greatest artists and poets, with all their creative genius, are in principle but children of larger growth.

Again, the development of simple experience to highest and completest ideation is the familiar road of science, as its history and its logic agree. The chemists and physicists started as babies with burning their fingers; and indeed wonderfully keep on doing so. And the child who has first thrilled to any story worth telling has reached beyond the immediate home-circle of folk-feeling, and begun initiation into the great emotional surges of life through history, even to those of the great religions. It is thus no mere crude materialism, but as the normal evolutionary process of humanity, that men have so often risen—and must ever rise—from very simple and even animal-like babes to the highest summits of achievement, and in all fields of the human spirit, imaginative, intellectual, emotional. And if so, to work out the steps of this evolution is the great problem before our evolutionary psychology; and to apply such science is the corresponding task of education, as it becomes truly educative.

But now our problem, as biologists, is simpler, yet more obscure also. All these high levels of human achievement are distinctly and intelligibly differentiated from each other, however also complexly and variedly combined in individuals and their achievements. However we may be convinced that the boy is father of the man, child-study is of later date than biographical criticism, and more difficult too. Still more difficulty appears as we descend in the animal scale. For here it is just as with physiology, which is far more easily investigated and understood in the specialised functioning of well-developed and clearly differentiated organs than in the ovum, or in the protozoon, elemental and ancestral though it be.

Hence, too, our comparative psychology has begun later than human psychology; and is obscurer also. For when our own so largely animal-like babes perplex us, what of incomparably more babe-like animals? It is a great step to be reaching an understanding of the higher ape-minds, as more or less on a level with the child's in very early years; but how much harder to make much out of the behaviour of creatures simpler and simpler still!

Yet something (indeed, often much) of *senses* are manifest in them; and experience is claimed even for Protozoa, beyond Loeb's mere tropisms. Though the old stories of animal intelligence are being critically investigated, and often with serious abatement of their wonders, there yet remains, as the biopsychologic evolutionist must indeed be prepared for, some readjustment of experience towards purposiveness and action. As for the feelings, and even their expression, the path opened by Darwin's classic "Expression of the Emotions" has been followed downwards; and though he, of course, dealt only with higher animals, no one has fixed any limit on the descending scales of life, for their existence, any more than for their origin.

Here we are greatly helped by the psychology of the subconscious, which has long been in progress; and which even arose among the physiologists, before the psychologists took hold of it. Yet no advance in our conceptions of the mental aspects of life is more characteristic of our time; witness the step from that mere dim perception (if not merely reception) almost grudgingly granted to the lowest forms of life, to the *élan vital* of Bergson, and again to the active *libido* of the psycho-analysts, and so on: in short an *urge* of life, and this viewed as psychic, and not merely as plasmic, though this as well. Nunn's *hormé* also seems a convenient term, and likely of widening adoption.

Whatever be the mysteries of life, it is undeniable that life is not something in the organism isolated from its environment, for such organisms are dead; its essential condition is that of traffic with the environment, in incessant alternation of give and take. Its response to stimulus is not merely like the heating of iron by the hammer, nor yet indefinite, like the flickering and spreading of a flame: it exhibits special activities, but these as part of the association of organism and environment together as life. All these functions are maintained in their relation as definite life-processes or sub-processes and their functionings all combine, thus successfully resisting death as long as may be. Every organism's general life-process, life-history, is thus a succession of complex yet unified scenes, which combine into its life-drama. And this is of no small complexity; since all the advances of biology are but partial, though increasing, discernments of it.

So here, and in the conception of the urge of life, was the profound

intuition of Lamarck; who was long too belittled by the predominantly mechanistic attitude impressed upon later thinkers by the industrial age, and its corresponding advances in the physical sciences, preliminary to biology, and still too often claiming practically to supersede it; albeit with fruitful results of their own. The familiar criticisms, of his too simple faith in the heredity of the blacksmith's potent biceps, or of his too naïve presentment of the giraffe lengthening his neck, were of course needed: yet what he was really striving to express for evolutionary change is nowadays being restated, in terms of the subconscious urge of life, its hormé, its libido, or whatever else we may come to call this. In a word, Bergson (with many more concrete naturalists) is essentially neo-Lamarckian.

That the mechanistic physiologists, the neo-Darwinian naturalists, usually remain of their traditional way of thinking is not, of course, denied. Weismann's "all-sufficiency of Natural selection" has still its sturdy supporters, and these often doing excellent work upon those lines; as notably in their criticisms of the too long persistent interpretation of animal ways by the earlier ecologists in terms of the older psychology of their times. But do they not also too much leave out of consideration this later psychology, and even thus offer us a one-sided account of life, mechanistically physiological, and thus practically without adequate psychological aspect or content at all? Hence it is surely reasonable to invite their consideration and criticism of such endeavours towards reconciliation as Haldane's, Russell's above outlined, or our own in these pages.

CHAPTER VI

ORGANIC FORM AND ARCHITECTURE

(Morphological)

DEFINITIONS.—Morphology is the science of the *structure* of living creatures, the study of all the statical aspects of organisms. Thus it is the correlate of physiology, which is concerned with activity or function, with vital dynamics and chemical reactions. One may distinguish three chief tasks: (*a*) the description of the organism as a whole and in all its parts—descriptive anatomy, becoming histology when it deals with microscopic structure; (*b*) the comparison of one organism with another, so as to discern the deep resemblances on which a "natural" classification is based (comparative anatomy and histology); (*c*) the discovery of laws of organic architecture, the "principles of morphology". In the third task the morphologist joins hands with the evolutionist. The material of morphology may consist of creatures that were killed yesterday, or of creatures that became extinct and were fossilised millions of years ago; in the study of structure age makes no difference except that the analysis of fossils is usually more difficult. Furthermore, since the morphologist may study an unhatched chick, a tadpole and a caterpillar as well as a fowl, a frog and a butterfly, no hard lines can be drawn between anatomy and descriptive embryography, the difference being largely that the embryologist is looking at the stages, to which he applies anatomical and histological methods, as chapters in a life-history. And while it is true that the anatomist is focusing attention on structure not on function, it would be a very wooden study that regarded the life and environment of the organism as irrelevant. An animal's shape, for instance, must be thought of in relation to its movements in a certain environment, and how can anyone intelligently dissect the heart without considering its way of working? While it remains true that the emphasis in morphology is on the *statical* aspects, whereas the emphasis in physiology is on the *dynamical* aspects, the study of structure and function, of function and structure, must go hand in hand; and now increasingly do so.

LEVELS OF MORPHOLOGICAL ANALYSIS.—As already indi cated, the physiologist studies the organism (1) as an intact unity with certain habits or ways of living, (2) as a living engine with parts or organs specialised for certain functions, (3) as a complicated web of interwoven and interacting tissues, (4) as a city of

co-operant cells, and (5) as an integrated multitude of protoplasmic vortices in which diverse chemical reactions are going on with great rapidity. It is the same in morphology, for there are necessarily the same levels of structural analysis.

(I) The organism must be studied as an intact unity with a certain shape and symmetry. (II) Scalpel in hand, in the case of animals, the anatomist must disclose their larger organs, such as brain and sensory structures, heart and lungs, liver and kidneys. (III) With hand lens and microscope he must then unravel their web of tissues—nervous, muscular, glandular, and connective. (IV) But every component cell is a microcosm with great intricacy of detail; and (V) the protoplasm itself has its colloidal film-work and ultra-microscopic particles.

FORM AND SYMMETRY.—The shape of a great mass of crystals, as in a snow-wreath, is partly determined by the molecular constitution of the material, and partly by the environmental influences that play on it while it is being formed. Similarly, but in a more complex way, the form and shape of an organism depend on the nature of the protoplasmic material, and on the surrounding influences. For some reason that we cannot at present analyse, a particular kind of sponge or coral has to make certain forms of spicules, which determine the general architecture of the skeleton; on the other hand, the shape of the sponge or the coral often varies, according to the currents that play on it, or the substratum on which it develops and grows.

As regards symmetry, animals may be grouped as (*a*) radial, (*b*) bilateral, and (*c*) asymmetrical. (*a*) In a radially symmetrical animal, such as a jellyfish, the body can be divided into two mirroring halves by a number of vertical planes. It is symmetrical around a vertical median axis, and it cannot be said to have a right or a left side. This is the symmetry of the frequently occurring gastrula stage in development, and the symmetry of the hypothetical, but highly probable, gastræa ancestor of multicellular animals. Going farther back still, we find radial symmetry in a Protozoon colony like Volvox, with hundreds to thousands of cells united in a sphere, though as a matter of fact one pole of the sphere is almost always in front in the beautiful spiral swimming. Farther back still, many a unicellular organism, both among Protozoa and Protophytes, is radially symmetrical; very often it is spherical or oval in shape.

It is necessary to distinguish, from thorough radial symmetry, what may be called superficial radial symmetry. Thus although a sea-anemone is a tubular animal, superficially quite radial, there are only two cuts that will divide the body into two identical halves, namely (1) the vertical cut which passes through the two ciliated gullet-grooves or siphonoglyphs, and (2) the vertical cut at right

angles to the former, which will leave one siphonoglyph for each of the halves. Similarly, though a sea-urchin or a starfish is superficially radial, and has some radiate arrangement of internal organs, there is only one cut that will yield perfectly mirroring halves, namely, the cut that passes through the centre of the madreporic plate by which water enters the hydraulic locomotor system. In the same way, while a typical two-tentacled Ctenophore, such as Hormiphora or Cydippe, is in a general way radial—a singularly beautiful, transparent, free-swimming globe, there is a hint of bilaterality in the position of the two tentacles and the sheaths into which they can be retracted. This hint of bilateral symmetry is more pronounced in some other Ctenophores, such as Venus's Girdle (*Cestus veneris*), and this is interesting in relation to the plausible theory that the bilateral Turbellarian worms evolved from creeping Ctenophores.

Radial symmetry is suited for a sedentary mode of life, and the capture of food by means of tentacles surrounding the mouth; and also for an easygoing life in the Open Sea, where the movements are not energetic and tend to be somewhat aimless. It is rarely of survival value to an animal like a Medusa to be able to move rapidly in a definite horizontal direction, but it is interesting to notice that it is often important for the Ctenophores that most of them are able to move rapidly downwards, for this saves their extremely delicate body from being broken on the surface in stormy weather. Most of them descend into quiet water before the waves begin to break.

(*b*) In bilateral symmetry, such as that of an earthworm or a mussel, a fish or a bird, there is only one plane that divides the body into two mirroring halves—the vertical plane passing through the middle of the dorsal and ventral surfaces. It is characteristic of most animals above the level of Cœlentera. It is obviously better suited than radial symmetry for vigorous locomotion, as in pursuing food, avoiding enemies, and chasing mates. With bilaterality is associated the evolution of a head-brain, which probably arose racially, as it arises individually, from the local differentiation and insinking of neurons at the anterior end of the body, where the maximum number of stimuli will be received. We do not mean that the stimulation produced nerve-cells; differentiation cannot be accounted for as simply as that. We mean that, given the nerve-cells, those bilateral animals that varied in the direction of having them in the head would have a marked advantage. It should be noted that among the Turbellarian worms, in which a head-brain first appears, the chief ganglion often lies near the middle of the ventral surface.

(*c*) Among many animals that are on the whole bilateral there is a departure from perfect symmetry. Thus the upturned right

valve of an oyster is flatter and thinner than the downturned, externally very convex left valve. But one would not because of such minor inequalities exclude an oyster from among the Bilateral animals. It is very different, however, with a snail, and with the majority of Gastropods, for in these there is an early acquired asymmetry. In connection with the enclosure of the body in a protecting shell there is a spiral coiling of the viscera; moreover, there is a deep-seated torsion of a large part of the body to the right-hand side forwards; so that the anus, the excretory pore, and the genital aperture come to lie anteriorly towards the mouth—a twisting which is partly connected with the presence of an enclosing shell. The torsion of the snail's body is a difficult problem, beyond our scope here, but it is plain that the asymmetry does not in any way interfere with the creature's efficiency. Among other markedly asymmetrical animals, which cannot possibly be divided into mirroring halves, may be mentioned the typical ascidians or sea-squirts.

Hermit-crabs are interesting in this connection because they are bilateral in their young stages, and become asymmetrical in their abdominal region, and usually as to their great claws (chelæ), when they begin to ensconce themselves in borrowed Gastropod shells. The lop-sidedness of the tail may be *in some degree* an individual modification, impressed on each generation, but the experiment has not been made of supplying the young stages with nothing but symmetrical tubes. On the other hand, an Indian Ocean form, *Pylocheles miersii*, which inhabits pieces of bamboo stem, is perfectly symmetrical, even as regards the abdominal appendages and the chelæ which form the door of the house. This would suggest that the asymmetry of ordinary hermit-crabs is altogether an individual modification. That this is not the case seems to us to be indicated by the interesting asymmetry in the abdominal region of the Stone-crabs, Lithodes, which do not borrow a shell, and of the very distantly related Robber-crab (*Birgus latro*), which sometimes protects its tail in the broken shell of a coco-nut. Now experts on Crustaceans seem to be agreed that the Stone-crabs and the Robber-crabs are descended from hermit-crabs (Paguridæ) that live in shells, though from different stocks of these. But since these two types show distinct traces of the Pagurid asymmetry, the case indicates either (*a*) that this feature cannot be wholly an individual modification, or (*b*) that an acquired somatic modification may be in some measure transmitted to forms in which the modifying influence does not operate. (See section on "the transmission of acquired characters" in the chapter on Evolution.)

Changes of symmetry in the course of the lifetime are not uncommon. Thus all the bony flat-fishes (like plaice and sole) are bilaterally symmetrical in their early larval stages, and the free-swimming Tunicate larva is also bilateral. The conditions in many

Echinoderms are complex: the larvæ may be bilateral, like the "painter's easel" Pluteus; the adults may be radial superficially and in some measure internally; but if in strictness we insist that a sea-urchin and a starfish are bilateral (considering the madreporic plate and so forth), and if we further recognise the obvious bilaterality of a heart-urchin (e.g. Echinocardium and Spatangus), we have to notice at the same time the curious fact that the plane of the adult's bilateral symmetry is not the same as the larva's!

It may be noted that while the asymmetry is usually between right and left sides, this is not the only possibility. Thus the bilaterally symmetrical Lamp-shells or Brachiopods—which have a slight superficial resemblance to the bilaterally symmetrical bivalve molluscs, though in no way related to them—often show a marked inequality between the dorsal and the ventral valves, contrasted in their position with the right and left valves of Lamellibranch molluscs.

Many free-swimming animals, from Paramœcium to larval Ascidians, move in a helicoid spiral, as man does in a fog or when swimming blindfolded. Though this is not due to any obvious inequality, e.g. of legs, it is probably correlated with some deep and subtle asymmetry.

ORGANS.—Any well-defined part of an organism that has a dominant function and some measure of independence may be called an organ, as in the case of brain and heart. But many an organ, such as leaf and liver, has numerous functions. There is something to be said for using the term organella for a specialised part of a unicellular animal or plant, such as a locomotor flagellum or a contractile vacuole or a pigment-spot.

As to historical emergence, it can hardly be said that Sponges or Porifera have *organs*; they remain at the level of histonal or tissue animals. The first organs in the Animal Kingdom are seen in the Phylum Cœlentera, where one may find not only an enteric cavity (or food-canal), which might be claimed for sponges, but in some cases, like sea-anemones and true jelly-fishes, a specialised gullet and digestive filaments. Reproductive organs, sense-organs, nerve-ganglia, and other specialised parts soon make their appearance. After the establishment of a food-cavity—the "archenteron" of the gastrula embryo in the individual, the enteron of the ancestral gastræa for the race—the first organs to appear were probably the reproductive organs or gonads. Thus a very simple animal like Microhydra has a food canal and gonads, but no other organs at all, not even tentacles! If we rank the food-canal as the first organ, we may put the gonads second. It has been suggested, however, and there is interest in the speculation, that if multicellular evolution started from a hollow ball of cells as in Volvox, the central cavity

might be a primitive brood-chamber or gonocoel, as it is indeed in the type mentioned. A food-canal could be dispensed with if the peripheral cells were holophytic or if they were able to capture food-particles by means of flagella.

But whatever the precise order of their appearance may be, there is no doubt that in the racial evolution of animals, as now in their individual development, organs appear gradually. Before there were definite nervous cells there was irritability, as we see in the muscle-cells of some sponges; before there was nervous tissue, there were scattered nerve-cells, as in Hydra; before there were nervous organs there was a nerve-network or nerve-plexus, as in sea-anemones. In other words, functions arose and still arise before organs. The attainment of organs implies specialisation of parts, a concentration of functions in particular areas of the body, and a certain degree of circumscribed independence, though it is an even larger fact that the organs of the body work into one another's hands. Among plants there are fewer definite organs than among animals; the lower plants or Thallophytes hardly rise above the level of histonal or tissue organisms; and this condition lingers even among higher forms, though these have also attained to definite organs, such as leaves, roots, shoots, and the parts of the flower. A tendril, a fly-trap, the pitcher of a Nepenthes, a nectary, may be taken in illustration of plant organs. Morphologically regarded, however, plants do not rise beyond the structural level of Cœlentera in the Animal Kingdom.

Differentiation and Integration.—Many a sponge has an intricate structure, but one piece of its body is like any other piece. Compared with an animal of higher degree, such as a fish, it shows very little local division of labour or *differentiation*. In the fish there are many specialised parts, while the sponge is very homogeneous in spite of its intricacy. In many cases a portion of the sponge's body can be cut off and bedded out, with the result that it grows an entire sponge. This is not possible with a more differentiated animal. If the comparison be permitted, a railway engine of 1930 shows great differentiation compared with Stephenson's first locomotive of 1814. Differentiation is the structural side of division of labour.

But when the contrast between sponge and fish is pressed farther, it is plain that the fish is much more of a unity than a sponge. Its parts are more closely knit together and more adequately subordinated to the life of the whole. This kind of progress is called *integration*; it means a unifying, co-ordinating, and harmonising of the parts of the body. The modern locomotive is much more under control than the locomotive of a century ago; it is more integrated. In the physiological chapter the question rises how the integration

of an animal is effected (*a*) by the nervous system which makes part thrill to part; (*b*) by the common fluid medium of the body (usually the blood and the lymph) from which all parts take and to which all parts give; (*c*) by the special "humoral" function of the blood, in distributing the chemical messengers or "hormones" which play a very important rôle in regulating the various bodily functions. But we wish to point out here that the architecture of the body often plays a humble, yet important, part in integration. The possession of an axis, such as the backbone, implies some unification of bodily movements. Similarly among backboneless animals the presence of an exoskeleton—such as the cephalothorax shield of a crab, in which

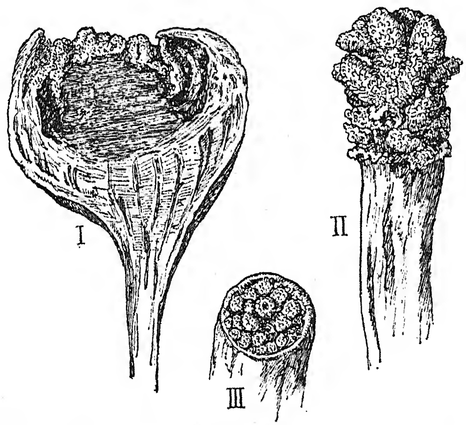


FIG. 93.

A Peculiar Type of Alcyonarian Coral, Studeriotes, in which polyp-bearing branches can be entirely retracted within a protective densely spiculose cup seen in section in I. In another species (II) the cup-portion is not so much expanded, yet the polyp-bearing branches are entirely retractile (III) into the upper portion of the stalk. From specimens.

many different muscles find insertion—secures the same consolidation. So with the test of a sea-urchin, or the shell of a snail, or the chain armour of a Bony Pike, or the carapace and plastron of a tortoise, or the bony shields and rings of an armadillo; they may all be credited with great measure of skeletal integration.

It will be understood, then, that the two standards in reference to which we decide the relative levels of organisation reached by different animals (or plants) are differentiation and integration.

CORRELATION OF ORGANS.—It is of the very nature of an organism to be *one*; many members but one body. The various organs are all partners in the business of life, and if one member changes, others may also change. This correlation of organs is

especially true of those that are closely bound up together in connection with some function; thus if the breathing organs are not doing their work sufficiently well, there will be a strain on the heart to send more blood through them. There is also likely to be a correlation between two structures that have developed and evolved together, as in the case of the brain and the eyes, the stomach and the liver. A new departure or variation due to some initial germinal disturbance may bring a correlated variation in its train, especially in a structure which is historically associated with the first. Or a variation in the activity of a ductless gland may affect several distinct structures which respond to the particular hormone secreted.

The morphological aspect of the "correlation of parts" was prominent in the work of Cuvier (1769–1832), to whom the idea was a guiding principle, though he failed—indeed refused—to see its chief import. What impressed him as a comparative anatomist was that certain structures go together, or, on the other hand, that certain structures exclude one another. If a mammal "chews the cud", it will have a "cloven hoof"; if the embryo of a Vertebrate has an allantois, it will not have gills; if a fish is a cartilaginous fish, it will have a spiral valve in its intestine; if a reptile has a bony carapace, it will not have a breastbone, and so on. Cuvier had a clear vision of the fact that an organism is a unified integrate, but he exaggerated terribly when he wrote: "A claw, a shoulder-blade, a condyle, a leg or arm-bone, or any other bone separately considered, enables us to discover the description of teeth to which they have belonged; so also, reciprocally, we may determine the form of the other bones from the teeth. Thus commencing the investigation by a careful study of any one bone by itself, a person who is sufficiently master of the laws of organic structure may, as it were, reconstruct the whole animal to which that bone had belonged." What Cuvier missed, being a determined opponent of Lamarck's heretical evolutionism, was the illuminating idea that these correlations depend on a common ancestry, in which similar variational changes have taken place in different parts of the body. If we find a recent mammalian skull with an inflected angle of the lower jaw, and with the jugal bone continued backwards to share in making the glenoid fossa for the articulation of the lower jaw, we may safely make a somewhat precise technical statement in regard to several peculiarities of the teeth, even though they have all fallen out. For Marsupials are the only animals which show in one skull the two peculiarities first mentioned, and all living Marsupials that have been studied have certain dental peculiarities. The correlation or simultaneous occurrence of these two sets of peculiarities depends on the presumed fact that Marsupials are descended from a common ancestral stock, which probably had the beginnings at least of the peculiar features. We do not doubt that there may be in certain

cases a developmental reason why two sets of peculiarities should go together, being consequences of a common cause, or outcrops of a common physiological tendency; but this has not been worked out except in a few cases. In many cases it seems extremely improbable. Thus if we found a recent Marsupial skull, and could say—from the geographical distribution perhaps, or from the dentition—that it did not belong to the families of opossums or of Dasyures, we could safely say that the female would have a pouch or marsu-

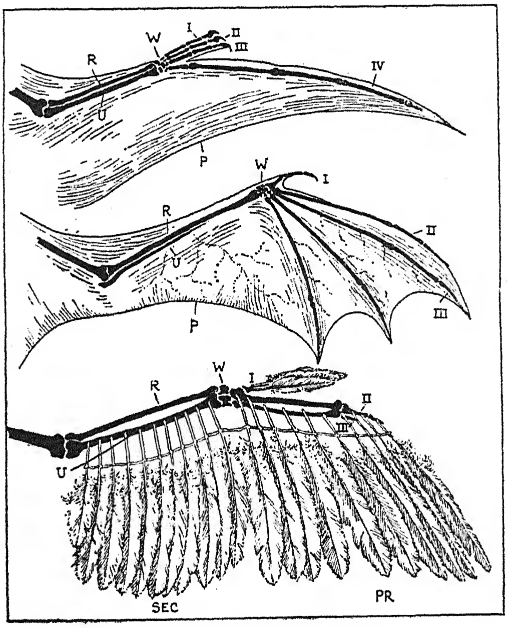


FIG. 94.

To illustrate Homology. The wings of Pterodactyl (above), Bat (middle), and Bird (below). From specimens. All are transformed fore-limbs. R, radius; U, ulna; W, wrist; I–IV, fingers; P, patagium of skin; PR, primary feathers; SEC, secondary feathers.

pium. But a physiological or embryological correlation between the skull and the pouch is highly improbable!

HOMOLOGY AND ANALOGY.—Organs that arise from the same germinal layer have something in common; thus the scales of Reptiles, the feathers of Birds, and the hairs of Mammals, so very different from one another in structure, are alike in being entirely epidermic differentiations, though nourished by the underlying dermis. But when organs develop in the same way from the same germinal layer or layers, they have still more in common; thus the swim-bladder of a fish and the lung of a frog are both hollow out-

growths from the anterior region of the food-canal; they are lined internally with endoderm and covered externally with mesoderm. But when organs have not only the same general development but the same fundamental structure, their resemblance is still closer, and they are said to be *homologous*. Thus the fore-limb of a frog, the fore-paddle of a turtle, the wing of a bird, the flipper of a whale, the wing of a bat, the fore-leg of a horse, the arm of man, are all homologous. They start in development in the same way as minute lateral buds, and they show the same fundamental bones, muscles, nerves, and blood-vessels. Homology is general resemblance in development and in fundamental structure, entirely irrespective of what the use of the part or organ may be.

Different parts of the same animal may be homologous, and they are termed serially homologous, when they are several times repeated. Thus the lobster's nineteen pairs of appendages (unless possibly the first two) are serially homologous, although they show great diversity of function and of final form. It was a great step long ago when Savigny showed that the three pairs of mouth-parts or "jaws" are homologous with the insect's legs, being, in a word, "appendicular". But the idea of homology is the same whether the parts compared are in one animal or in different animals; hence one of the memorable diagrams in the history of zoology is that in which Belon (1555) placed side by side the very different skeletons of bird and man, and indicated the homologies of their various bones.

Morphological Theory of the Flower.—Here we may refer to one of the clarifying ideas in morphological botany—that the flowering plant consists of an axis bearing various homologous appendages of a leaf-life or foliar nature. The cotyledons or seed-leaves, the radical and cauline leaves at the base and higher up the stem, the bud-scales and the bracts, besides the sepals and petals, the stamens and carpels, may all be regarded as homologous. It is for the young student a never-to-be-forgotten lesson to make and draw a series from the outer scales to the young palmate leaves in the opening bud of the horse-chestnut, or a series from green sepals, through petals, to the stamens of the water-lily. The stamens and carpels are no doubt the bearers of spore-forming organs (anthers and ovules), but in themselves they are foliar, as Goethe said. This is indicated not only by their mode of development, and by the occurrence of transitions between petals and stamens, but also by the resumption of more leaf-like features when the flower relapses into vegetativeness and becomes "double", the stamens being in many cases replaced by petaloid structures.

The idea of the fundamental identity of floral parts and leaves is an old one, and was clearly expressed by Linnæus in the aphorism *Principium florum et foliorum idem est.* Even earlier there were

anticipations on the part of Cæsalpino, Malpighi, and Joachim Jung; but it is not always clear whether it was believed that a vegetative leaf might actually become a floral leaf, or whether no more was suggested than the possibility of *thinking* of leaves and floral parts as "metamorphoses" of the organs of an ideal "archetypal" plant.

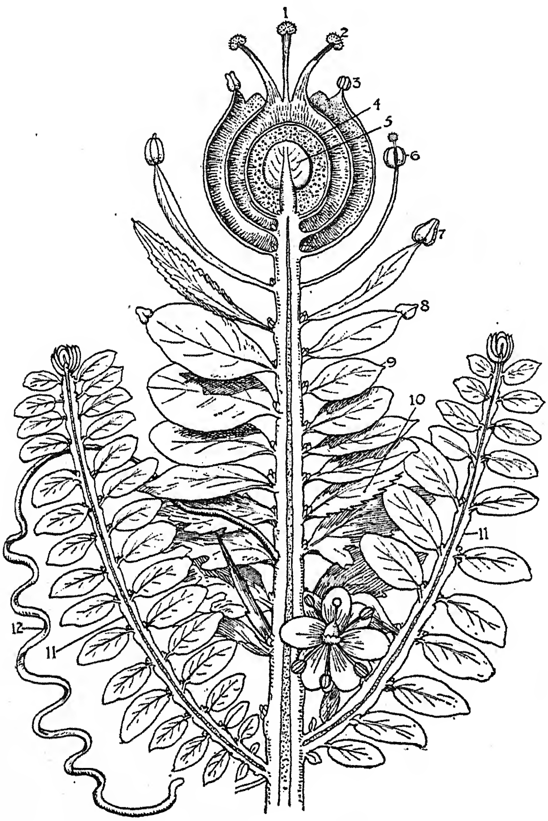


FIG. 95.

Part of Goethe's Figure of the Homologies between Floral Parts and Foliar Structures. 1 and 2, the stigmas of carpels; 3, 4, walls of the seed-box; 5, the seed-leaves or cotyledons; 6, typical stamen; 7, slightly petaloid stamen; 8, intermediate between stamen and petal; 9, petal; 10, sepal; 11, a compound leaf with pinnules; 12, a tendril transformation of a leaf.

But there was no dubiety in the mind of Caspar Friedrich Wolff (1733–1794), who came to the subject as a zoological embryologist, and showed that the various "appendicular organs", whether ordinary leaves or floral parts, have a similar mode of development from the growing point of the stem. He wrote firmly: "In the entire plant, whose parts we wonder at as being, at the first glance, so

extraordinarily diverse, I finally perceive, after mature consideration, and recognise nothing beyond leaves and stem (for the root may be regarded as a stem). Consequently all parts of the plant, except the stem, are modified leaves." But Wolff went further and raised the question—still before us to-day—*how* the modification or "metamorphosis", as it was then called, had come about. "We must investigate the causes which so modify the general mode of growth as to produce, in the place of leaves, the parts of the flower." Wolff's own theory was that the transformation was due to a diminution of vegetative vigour (*vegetatio languescens*).

More than twenty years after Wolff, the poet Goethe was led "through long prosecuted studies" to the same conclusion. In his famous essay of 1790, *Versuch die Metamorphose der Pflanzen zu erklären*, the doctrine of the fundamental unity of floral and foliar organs is clearly enunciated, and supported by arguments from anatomy, development, and teratology. All the appendicular organs of a plant are thus modifications of one fundamental organ—the leaf, and all plants are in like manner to be viewed as modifications of a common type—the *Urpflanze*. Wolff was ahead of Goethe in his developmental evidence of "metamorphosis"; but the morphology of his day was not sufficiently advanced to give him any clear idea of what it was that had been the subject of all the supposed metamorphosis. He had not a well-defined morphological and embryological conception of the leaf. He felt this himself, as he frankly says, and he was also puzzled by the possibility of reading the facts in two ways: Has the metamorphosis been from vegetative leaf to floral leaf, or has it been in the opposite direction? "For", as he said, "we can as well say a stamen is a contracted petal as we may say of the petal that it is an expanded stamen; or that a sepal is a contracted foliage-leaf, as that a foliage-leaf is an expanded sepal."

It is clear nowadays that the stamens and carpels are not simply transformed foliar organs, as might be said of sepals and petals, for they bear specialised spore-making organs or sporangia, namely, the anthers and the ovules. But while some botanists regard the spore-producing leaf or sporophyll as a transformed foliage-leaf, there are others who maintain that the foliage-leaf is a transformed sporophyll which has become sterile. As Vines says, "The view that the foliage-leaf is the primitive leaf-member, and that the floral leaves are its derivatives, is based upon the fact that, as a rule, the vegetative precede the reproductive organs in ontogenesis. The opposite view, that the most highly specialised floral leaf, the sporophyll, is primitive, is based upon the fact that, phylogenetically, the reproductive precede the vegetative leaves." In any case, the general homology of folial and floral organs is admitted.

Note on Morphology of Vascular Plants.—Nearly a century ago, when the colonial nature of so many Hydrozoa, corals, Bryozoa,

ascidians, etc., was becoming clear, the attractive speculation that the branching growth of plants might be similarly interpreted was ventured by Gaudichaud, who argued that each leaf, with its appropriate portion of stem, should be considered as the essential unit, which he called the "phyton"; and which, by its budding of new ones, develops the vegetative system, from which again, as a crowded and integrated grouping of phytons, appeared the flower. The familiar view of the stem developing its own leaves, however, prevailed; with the fascinating homologies of bud and shoot, so intelligibly condensed to bulb, or differentiated to flower.

Yet now we have in recent years the strenuous, elaborate and undeniably skilful developmental and histological labours of M. Chauveau, who so far returns to Gaudichaud's theory, yet with modification; and this with a refinement of investigation and vigour of argument which compel respect. Though most botanists remain as yet unconvinced, it is not easy for them or us to disprove his critical explanations of their conservatism. His unit, and thus miniature plant, he calls the *phyllorhiza,* essentially a leaf with rootlet. Repeated budding and coalescence give rise to the stem, which is thus no longer viewed as primary, but as a secondary formation. But all that we are concerned with here is to *illustrate* morphological enquiry.

ANALOGY.—When organs have a functional resemblance, discharging the same chief rôle, they are said to be *analogous,* whether they are homologous or not. Thus lungs and gills are analogous, both being organs of respiration, but they are not in any sense homologous; thus a Vertebrate's lung is a hollow outgrowth from the anterior part of the food-canal and the gills of a typical fish are feathery structures growing out from the sides of gill-clefts, which again are outgrowths from the pharynx. There may be some deep similarity between a lung and a gill-cleft, since both are outgrowths from the alimentary canal, but there is no possibility of homologising a hollow bag with a group of feathery filaments.

The first clear focusing of the contrast between homology (developmental and structural resemblance) and analogy (functional resemblance) is due to Sir Richard Owen. Three of his illustrations may be given:

(*a*) the wing of a bird and the arm of man are homologous, but not analogous;
(*b*) the wing of a bird and the wing of a butterfly are analogous but not homologous; both are organs of true flight, but they are entirely different in structure and development;
(*c*) the wing of a bird and the wing of a bat are at once analogous and homologous, for both are organs of true flight, and both

are transformed fore-limbs. It would be pedantic to make much of the backward continuation of the bat's wing beyond the fore-limb boundary.

In some plants the function of a leaf is discharged by a flattened shoot, which looks extraordinarily leaf-like, as in the case of the floating discs of the Duckweed (Lemna). This is a difficult case, for the internal structure of the flattened shoot is also adapted to the leaf-function that has been assumed. Yet it is impossible to admit homology when the mode of development is quite different. Moreover, in the case of the duckweed, the leaf-like floating disc bears very minute flowers on its margin, and gives off a long root on its under surface. A tendril may be part of a stem or part of a leaf or a transformed stipule, yet the function is the same throughout. A prickle on a rose-bush is an integumentary structure, comparable to a hair; the spines on the holly are moribund projections on the margin of the leaf; and the thorns of the hawthorn are abortive branches—often with tell-tale leaves.

HOMOPLASTY OR CONVERGENCE.—In 1870 Lankester suggested the desirability of distinguishing *homogeny*, or homology due to common descent, from "homoplasty", or resemblance due to the occurrence of similar adaptations in unrelated forms. He defined homoplasty as "that close agreement in form which may be attained in the course of evolutional changes by organs or parts in two animals which have been subjected to similar moulding conditions of the environment, but have no genetic community of origin to account for their close similarity in form and structure". The idea was subsequently extended to the form of the entire animal as well as the form of parts or organs. The term "convergence" was also suggested as a synonym for homoplasty, and Weismann defined it as "corresponding adaptations to similar conditions in animal forms not genealogically connected with one another". The matter deserves careful consideration. Convergence is now the usual term.

We have already noticed that structures that have no deep resemblance in development or in fundamental structure may perform a similar function, and may become *similarly adapted* to this function. Thus a stem structure (or phylloclade) in Asparagus, Butcher's Broom, Duckweed, and so on, may assume leaf-function and may become leaf-like not only externally, but to some extent internally. Such cases lead on to homoplastic resemblance or convergence—a resemblance between unrelated organisms or organs brought about by the fact that they have become similarly adapted to similar functions or to similar conditions of life. The majority of fishes are spindle-like or torpedo-like in shape, no doubt in adaptation to swift movement in the water, but there is no need for a

special term for this, since they are all fishes. What is illustrated is merely a similarity of adaptation among related forms. But it is different when the whales are brought into the comparison. This is homoplasty or convergence, for the similarity of adaptation occurs in forms that are in no way related, whales being mammals and thus very remote from fishes, as Aristotle clearly discerned over two thousand years ago.

It is very instructive to place in front of a student or oneself: (1) a burrowing Amphibian (say a Cæcilian like Ichthyophis), (2) a burrowing lizard (say an Amphisbænid or a slow-worm), and (3) a burrowing snake (say Typhlops), for the three specimens are superficially much alike in their worm-like shape. Yet a slow-worm is a lizard or Lacertilian, structurally very different from a snake or Ophidian, while the Cæcilian is far away from both of the others, being an Amphibian with, for instance, gills in an early stage of its development.

Sometimes the convergence is very superficial, for swallows and

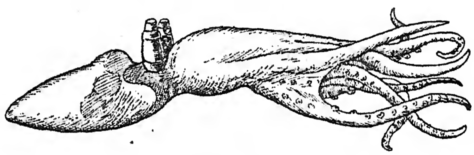


FIG. 96.
Deep-sea Cuttlefish, with "telescope eyes." After Chun.

swifts, which belong to very different orders of birds, are not very like one another except to the careless eye, and no one could really confuse a dolphin and a shark. Yet many serious errors in classification have been due to mistaking convergent resemblance for genuine homology, and this mistake ceases to be surprising when we examine convergences not between entire animals, but between parts. Thus there is a very striking detailed resemblance between the skull of an ordinary carnivore like a wolf and the skull of a carnivorous marsupial such as the Tasmanian Devil. Yet the resemblances concern adaptations (in teeth and crests and other features) which must have been evolved quite independently in the two cases. Similarly, the marsupial Wombat has its Rodent-like features and the "marsupial mole" its mole-like features.

But homoplastic resemblance is often much subtler than in the examples we have given, and the "telescope eyes" of some Deep Sea fishes and Cephalopods may be taken in illustration. "Telescope eyes" are elongated into cylinders, projecting like opera-glasses on the top of the head, with the lens relatively large and at a greater distance than usual from the surface of the retina on which the image is formed. These peculiar eyes are adapted to make the most

of the faint light of the great depths. Now the remarkable fact is that the "telescope eyes" of various types of deep-water fishes are closely paralleled by those of certain deep-water cuttlefishes, which belong to the phylum of molluscs. On two entirely different lines of evolution the same adaptation has been evolved; and the case is the more striking since the eyes of fish and cuttlefish develop in quite different ways, and are separated by important differences in detailed structure. The convergence that we are emphasising here is in the "telescope" structure; but there is also a remarkable superficial resemblance between fish eyes and cuttlefish eyes in general, though they develop in very different ways. For the fish eye is a "brain-eye", growing outwards from the brain to the skin, whereas the cuttlefish eye is a "skin-eye", beginning as a superficial insinking of skin. In the chapter on Evolution there is some consideration of the problem raised by the fact that the same *general* result may be reached in unrelated types by different modes of development.

Some other instances of convergence may be simply mentioned: the volplanes of various unrelated swooping mammals, among marsupials, rodents, and insectivores; the electric organs of the Torpedo and the Electric Eel, the one a cartilaginous fish or Selachian and the other a bony Teleost; the parachutes formed by the enlargement of the pectoral fins in unrelated "flying fishes", Exocœtus and Dactylopterus; the superficial resemblance between small rodents like mice and small insectivores like shrews, both adapted to making their way through narrow holes and tunnels.

DEVELOPMENT OF ORGANS.—In studying homologies, which form the basis for sound classification, it is necessary to consider the mode of development, and it may be useful here to introduce the general grouping for Vertebrate animals. (1) The outer germinal layer (the ectoderm or epiblast) gives rise to the epidermis and the structures it bears, to the nervous system, and to the foundations of the sense-organs. (2) The inner germinal layer (the endoderm or hypoblast) gives rise to the lining of the food-canal and of all its outgrowths (lungs, liver, pancreas, etc.), and to the skeletal rod, the notochord, which is folded off along the dorsal median line of the embryonic gut or archenteron. (3) The middle germinal layer (the mesoderm or mesoblast) forms skeleton, muscles, connective tissue swathings, the lining of the body-cavity or coelom, the muscular and connective sheath surrounding the food-canal, and such important organs as heart and kidneys. When an endodermic pouch grows out from the embryonic food-canal it will carry the ensheathing mesoderm with it, and thus all organs, like lungs and liver, that arise as diverticula of the mid-gut or digestive canal will be compounded of endoderm more internally and mesoderm more

externally. This is most clearly seen in the case of hollow organs, such as swim-bladder, lung, and allantois, which are *lined* with endoderm and externally *enveloped* with mesoderm.

There are few organs, in the usual sense of the word, that are altogether derived from one germinal layer, but the brain may be cited as almost entirely ectodermic; the mid-gut of round worms as wholly endodermic (without the mesodermic investment that is present in most animals); and the heart as wholly mesodermic. The eye is an instance of the intricate combination of ectoderm and mesoderm; the liver is an instance of the co-operation of endoderm and mesoderm; the sense-organs of a jellyfish illustrate the rare organogenic association of ectoderm and endoderm. The gonads or reproductive organs usually appear on the mesodermic

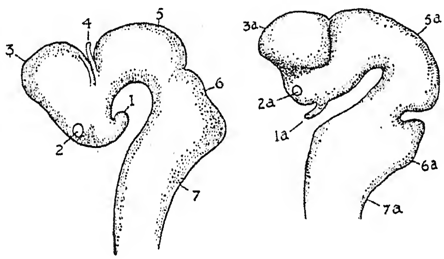


FIG. 97.

Two Stages in the Development of a Mammal's Brain. After Kupffer. 1, the olfactory lobe; 2, the developing eye; 3, the cerebral hemispheres; 4, the pineal stalk; 5, the optic lobes; 6, the cerebellum; 7, the medulla oblongata. In the figure to the right, the same parts (1*a* to 7*a*) are shown at a more advanced stage.

wall of the body-cavity, but in their essential part they arise from the early segregation of germ-cells, and so need not be thought of in connection with any particular germinal layer.

SUBSTITUTION OF ORGANS.—This idea, partly embryological, partly morphological, has to do with the way in which one organ or structure may lead on, individually and racially, to another which becomes its substitute. It was especially emphasised by Kleinenberg, and may be best explained by an illustration. In the early stages of all Vertebrate embryos, the supporting axis of the skeleton is the notochord—an endodermic rod folded outwards along the dorsal median line of the primitive gut or archenteron. In primitive types like the lancelet and the lamprey it becomes the persistent skeletal axis of the adult animal. It also persists to an appreciable extent in some fishes, such as sturgeon and mudfish. In most fishes, however, and in all higher animals, the notochord is

replaced by the vertebral column or backbone, which develops from a mesodermic sheath formed around the notochord. The notochord does not become the backbone; it is a temporary endodermic structure, around which the permanent vertebral column is constructed, as a tall brick chimney might be built around an internal scaffolding of wood. But what is the relation between the notochord and its substitute the backbone? Kleinenberg's suggestion is that the notochord in some way supplies the stimulus, the necessary precondition, for the development of the backbone. There is no doubt that one part affects another in embryonic development, sometimes by way of inhibition, as the growing point of a stem influences the buds just below; sometimes, by way of stimulus, as when the ingrowth of the ectodermic dental germ stimulates the development of a mesodermic papilla that forms the bulk of the tooth. The cerebral diverticulum that forms the foundation of the eye in Vertebrates grows till it meets the ectoderm, which then proliferates to form the lens; and whatever the nature of the stimulus may be, it is so powerful and specific that the experimental introduction of a fragment of optic vesicle underneath the epidermis of the very young tadpole will induce the formation of a lens in an entirely irrelevant situation, even beyond the limits of the head. It may be that an influence of this sort—possibly analogous to that of a hormone—is exerted by the endodermic notochord on the adjoining mesodermic tissue so that the development of a backbone is induced. The idea helps towards an understanding of the persistence of incipient evolving structures during the period before they are large enough to be of use. It also throws light on the prolonged persistence of dwindling structures which are relatively large in the developmental stages, but eventually of no functional importance.

CHANGE OF FUNCTION IN ORGANS.—One method of evolution is to effect a gradual change in the function of an organ. Different stages in the transformation can often be traced in a series of related types. Thus the Eustachian tube which leads from the outer ear-passage to the back of the mouth in all animals from Amphibians upwards is homologous with the first gill-cleft or spiracle of a cartilaginous fish, e.g. the skate, by which water enters the pharynx to pass out by the other gill-clefts, washing the gills on the way. There has been a notable change of function, for the Eustachian tube is not connected with respiration. In many cases, however, an organ has several functions, and the change that comes about is that a secondary function becomes in the course of time the dominant function. This idea of "Functionswechsel" received much attention from Dr. Anton Dohrn, the distinguished founder of the Naples Zoological Station, who spoke of it thus:

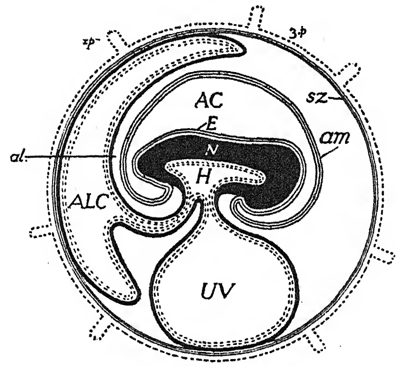


FIG. 98.

Diagram of the Fœtal Membrane in a Mammal. After Turner. E, ectoderm of embryo; H, gut, lined with endoderm; UV, umbilical vesicle or yolkless yolk-sac; AC, amniotic cavity; am, amnion proper; ALC, allantoic cavity, outgrowth from the posterior end of the gut or enteron; *al*, inner wall of the allantois; *3p*, the early ectodermal envelope or trophoblast, which gives off preliminary processes; *zp*, which attach the embryo to the wall of the uterus or womb; *sz*, the subzonal membrane, round the whole embryo; N, the mesoderm of the embryo.

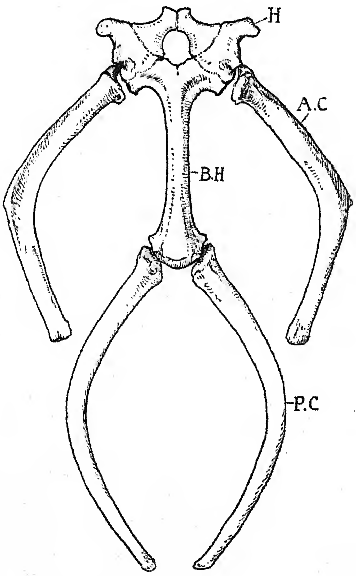


FIG. 99.

The Hyoid Apparatus of a Turtle. From a specimen. BH, the body of the hyoid (basihyal); H, anterior part of the hyoid arch; AC, anterior cornu, a transformed first branchial arch; PC, posterior cornu, representing a transformed second branchial arch. The figure illustrates that mode of evolution which consists in transforming an old structure into a quite new one of fresh significance. The use of the apparatus in the turtle is to afford insertion for muscles.

"Every function is the resultant of several components, of which one is the chief or primary function, while the others are subsidiary or secondary. The diminution of the chief function and the ascendance of a secondary function changes the total function; the secondary function becomes gradually the chief one; the result is a transformation of the organ." The contraction of every muscle is associated with an electrical change; the electric organ of the Torpedo is a richly innervated mass of transformed muscular tissue in which the production of electricity has become the main function. The structure known as the allantois, which forms a fœtal membrane (chiefly respiratory) round the embryo of reptile and bird, and a great part of the placenta of mammals, has for its homologue an unimportant cloacal bladder in Amphibians.

In this connection it should be noted that an organ may occasionally change its function in the course of individual development. The stalk of the embryo's allantois seems to become the adult's urinary bladder. The thymus gland, which develops in connection with the second embryonic gill-cleft or visceral cleft is largest in the human infant just after birth, and becomes smaller and smaller after the second year, until there is hardly a vestige left in adult life. It appears to be an organ in which lymph corpuscles are produced in the young animal, and then it dwindles. But an interesting fact is that it persists in those mammals that hibernate, and that it there changes its function, and becomes a fat-accumulating organ.

RUDIMENTARY ORGANS.—This term is usually employed to denote structures that have in the course of evolution dwindled so markedly that they have lost all functional significance The dwindling is inferred from the fact that they have well-developed and functional homologues in related types. Thus the traces of hind-limbs in whales are buried deep below the surface and are of no use; the third eyelid in man and monkeys is reduced to the small functionless fold in the inner corner of the eye; one of the lungs, usually the left, in snakes is represented by a small insignificant sac; the first gill (pseudobranch) of a Teleostean or bony fish is usually a small vascular patch, utterly unimportant. Other illustrations are given in some detail among the *Evidences of Evolution*. The best term for these structures is *vestigial*; for "rudimentary" is often (and better) used to mean incipient, and it is essential to the definition of the structures we are now discussing that they can be shown to be the useless remnants of structures that were once well-developed and functional. The electric organ on each side of the tail of a skate may be, in a large specimen, two feet long and an inch across, but it does not produce a shock strong enough to be felt by the human hand. But as its structure is not in any way degenerate, and as it is one of the last organs to be established in the course of develop-

ment, there seems good reason for regarding it as an *incipient* organ, which in the course of evolution may come to be of survival-value.

To be included along with vestigial structures in the strict sense are those which are present, *though apparently functionless*, only in the embryonic or larval stages. Thus the embryo whalebone whale has two sets of teeth which never cut the gum, but entirely disappear; and no use can be suggested for the posterior visceral clefts of the embryos of reptiles, birds, and mammals. The reason for not including a structure like the notochord has been already explained. But as another case in point we may mention the minute filamentous processes described by Boyden (1918) in the gill-clefts of the embryos of some reptiles, and of the fowl. They are too minute to be of functional significance, but they appear to be homologous with gill-*filaments*.

Perhaps it makes for clearness to keep by themselves those organs that are laid down in both sexes, but remain undeveloped in one. Thus the development of the milk-glands is normally arrested in the male mammal, probably because of the absence of the appropriate hormonic stimulation, or because of the presence of some hormonic inhibitent. There are cases, however, of some activation in the males, soon after birth, at sexual maturity, and under pathological conditions. Merriam gives a circumstantial account of male lactation in a hare (*Lepus bairdi*) (Hayden's *U.S. Geological Survey*, vi, p. 666). Similarly, but in a very different type, the first abdominal appendages in a male lobster or crayfish are strongly developed and are functional in reproduction, whereas in the female they are small, slender, apparently quite useless, and very variable. Many examples might be given; but the point seems clear, that organs much reduced in connection with sex-dimorphism should be kept apart from vestigial organs in the usual sense.

To complete this attempt to define vestigial organs more precisely, we may exclude *abnormal arrests of development*, when some structure, such as an eye, is spoilt in the making, and does not pass beyond very rudimentary expression. It is also desirable to exclude cases where the individual as a whole suffers marked degeneration in the course of its life. Thus the small ganglion of an Ascidian that lies between the inhalant and exhalant apertures is all that is left to represent the brain and spinal cord of the free-swimming larva; but it is hardly comparable to the vestigial gill seen inside the spiracle of the skate. Apart from the fact that the Ascidian ganglion shares in a degeneration which affects a great part of the animal, it is not a functionless structure. Similarly we should separate off the retrograded eyes of some cavernicolous crustaceans and fishes, which are minute even in the young stages. The retrogression cannot be seen in the individual lifetime, as in the Ascidians, for the eyes *begin* badly. It is more than arrested

development, where defective nutrition or some poisoning leads to a half-finished organ. But the need for great caution is illustrated by the case of the newt Proteus from the Dalmatian caves. In what must be called "normal" conditions, the darkness of the underground waters, the eyes remain minute and half-finished, and do not reach the surface. But if the larvæ are reared under red light in the laboratory, the eyes increase in size and in differentiation, and become seeing eyes on the surface of the skin.

Finally, from the group of vestigial organs there should be excluded all cases where some definite function persists, although there may have been notable reduction in the size of the structure. Thus the sting of a worker-bee is homologous with an ovipositor, which in turn may perhaps be referred back to a pair of abdominal

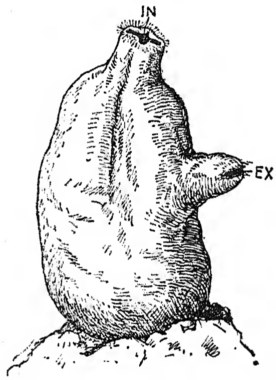


FIG. 100.

A Typical Tunicate or Ascidian. From a specimen. IN, inhalant opening; EX, exhalant opening.

appendages; but the sting of a bee is anything but functionless, and is an illustration of a transformed, not of a vestigial organ. It is, of course, very difficult to prove absolute uselessness; but where a definite function is discernible, the structure in question should not be called vestigial.

To sum up: there are dwindled functionless structures that persist in adult life, relics of well-developed and useful structures in ancestral types, e.g. the third eyelid in man. These are the most clearly defined vestigial structures or organs. In the same group may be included vestiges, like the whalebone whale's teeth, which do not persist beyond the period of embryonic development. But for clearness of definition it is desirable to separate off (*a*) incipient structures, (*b*) pathological arrests of development, (*c*) inhibitions of development associated with sex-dimorphism, (*d*) the outcome of general degeneration or retrogression, and (*e*) cases of transformation

in which there is also dwindling of size and sometimes a general simplifying of structure. The subject will be referred to again in connection with Evolution and Heredity.

CLASSIFICATION OF ORGANS.—The most natural arrangement of organs is not morphological, but physiological. They may be arranged according to the part they play in the life of the animal. Thus some have to do with *external* relations, and may be arranged as locomotor, prehensile, food-receiving, protective, aggressive, courting, and mating organs. Of internal organs, the skeletal structures are passive, compared with active organs like the heart, or the gizzard. Some are alimentary, others nervous, sensory, glandular, vascular, and so on; and a special rank must be ascribed to the regulatory, hormone-making organs, like the thyroids and the suprarenals. The essential reproductive organs or gonads,

FIG. 101.

Rattle of Rattlesnake, *Crotalus horridus*. From a specimen. This instrument is composed of a series of horny rings, added to at each sloughing, but continually dropping off terminally. A very rapid vibration produces a shrill whistle-like sound, which serves to warn off intruders too large to be of use. In the presence of a small rodent the rattling ceases. The rattlesnake does not hiss.

though also hormonic in Vertebrates, deserve to be placed by themselves.

But it is also of interest to classify organs according to the embryonic layer or layers from which they arise. Thus to the ectoderm must be referred all epidermic structures, such as hoofs and claws, all nervous organs, and much at least of all the sense-organs. The inner layer or endoderm forms at least an important part (the "mid-gut") of the food-canal, and the basis of all its outgrowths—lungs, liver, pancreas, and the like. The skeletal notochord is also endodermic. To the middle layer or mesoderm of the embryo must be referred the endoskeleton (except the notochord), the muscles, the connective swathings, the heart, the kidneys, the spleen, and so on. In many cases there is a dual origin; thus, as already stated, every outgrowth from the Vertebrate gut arises as an endodermic pouch, but carries the enswathing mesoderm out with it. The eye is essentially an ectodermic organ, but the mesoderm forms the firm outer layer or sclerotic, as well as the internal vitreous humour. Many relatively simple superficial structures such as horns are partly ectodermic and partly meso-

dermic. Ordinary teeth start from an ectodermic ingrowth (the enamel-germ) which becomes closely associated with a mesodermic papilla that forms such parts as the ivory and the pulp. In the development of the mouth and the gill-pouches there is a co-operation of ectoderm and endoderm. In the puzzling suprarenal body there is a medullary portion developed in connection with the sympathetic nervous system, and therefore ectodermic, and a cortical portion derived from part of the embryonic excretory system, and therefore mesodermic.

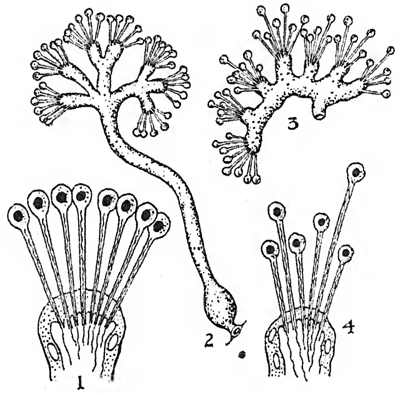


FIG. 102.

Excretory Cells in Various Types of Animals. 1, A tuft of solenocytes leading into an excretory tubule of a marine worm. The nuclei are marked by dark circles. After Goodrich. 2, The whole excretory tubule. 3, The inner end of a nephridium in Amphioxus. After Boveri. 4, A group of solenocytes from a nephridium of Amphioxus. After Goodrich.

TISSUES.—A tissue is an aggregate of similar cells with predominantly similar function or functions. Thus pieces of flesh (muscle), brain, fat, liver, and gristle may be mentioned as instances of animal tissue. Among plants, tissue may be illustrated by the transparent skin or epidermis, or by the green middle region of a leaf, by bark, wood, and pith, by the substance of a root or tuber, and so forth.

If we compare a body to a city, and the cells to the individual buildings, then a tissue may be likened to a street of similar houses or shops. As to an organ, it is more like a unified "quarter" of a city, such as the municipal buildings, the transport or the cleansing department, the industrial quarter, the power stations, and so on. The analogy is not to be pursued far, but it is useful for a first glance.

In the history of Biology, as we have already seen, the study of organs naturally preceded the study of tissues—which may be said to have begun, for practical purpose, with Bichât's *Anatomie*

Générale in 1801. The heart is an organ, with its chambers and valves, to be dissected out with scalpel and forceps, but Bichât penetrated to a deeper level of structural analysis, requiring the microscope, and studied the muscular tissue, the nervous tissue, and the connective tissue involved in the working of the organ in question, for Bichât was physiologist as much as morphologist. Indeed, in histology (*histon*, a tissue), it is not very profitable to try to separate the physiological and the anatomical aspects.

SURVEY OF ANIMAL TISSUES.—It is usual to distinguish (*a*) epithelial, (*b*) nervous, (*c*) contractile, and (*d*) connective tissue —the last very much of a lumber-room. Epithelium consists of a layer of relatively simple cells, often united by intercellular cementing substance, and sometimes with protoplasmic bridges running between one cell and its neighbours. In illustration may be mentioned the epidermis covering the outside of the body, the internal lining of the food-canal, the peritoneum investing the interior of the body cavity, the pulmonary epithelium lining the internal cavity of the lungs. The chief functions of epithelium are protective, absorptive, and glandular. In many cases the cells are columnar, like bricks placed on end, or like basaltic columns in miniature; the opposite extreme is seen in squamous epithelium, where the cells are horizontally flattened, like the slates on a roof. This is well illustrated by the flat cells which are continually being rubbed off from our lips; while the columnar cells lining our wind-pipe, with lashing cilia on their free surface, illustrate another very common type—ciliated epithelium. The cells of columnar and cubical epithelium usually divide into two in the plane vertical to the free surface, while others, such as those lining the mouth, divide in a horizontal plane parallel to the surface, thus giving rise to what is called stratified epithelium. What is shed in flakes in a moulting reptile is the outermost layer of the stratum corneum of the epidermis, which gradually dies away; and in snakes this is peeled off, from in front backwards, as a continuous "slough", bearing the imprint of all the scales, which are, of course, left behind. On the other hand, what is cast in a crab or lobster is a *cuticle*, which may be defined as a non-living and non-cellular renewable product of the underlying living skin. The slough of a snake once consisted of living cells, but the moulted cuticle of an Arthropod was never cellular.

In many cases the epithelium is markedly glandular, the cells making some non-living product or secretion at the expense of their living matter. When the epidermis of an ordinary fish, such as a skate, is microscopically examined, glandular epithelial cells, often shaped like tiny goblets, are seen at frequent intervals among the ordinary covering cells; and it is to their activity that th

abundant slime or mucus is due. But in the frog there are groups of glandular cells forming minute pits in the skin; in other words, the superficial glands are no longer unicellular but multicellular. The insinking of glandular epithelium forms narrow tubular glands in some types, swollen alveolar glands in others, and there are further complications, such as the abundant branching seen in the milk-glands or mammary glands, which are at first solid ingrowths, but become secondarily hollowed out. From scattered glandular cells in the earthworm's skin to the milk-glands of mammals is a long stretch, but, whether simple or complex, there is always the same essential glandular epithelium. Inside the gland-cell the living matter manufactures a secretion in the form of granules which turn into droplets, or of droplets from the first, and after it has become "loaded" with the secretion there is a rapid "unloading" or discharge, usually in response to a nerve-stimulus, but sometimes because the blood has brought an exciting hormone. In some cases a gland-cell makes one kind of secretion, like the mucus on the skin of a fish; in other cases there is a production of two secretions, as at the upper or cardiac end of a frog's stomach; or there may even be three, as in the cells of the pancreas. While we have referred in this outline to superficial glands in particular, most of the internal glands are, to begin with, also derivable from glandular epithelium. Thus the pancreas, the most important digestive organ in the body, is in the embryo a little pouch of the primitive food-canal, with a lining continuous with the glandular epithelium of the duodenum—the first part of the intestine.

NERVOUS TISSUE.—In sponges, which illustrate the beginnings of animal tissues, there are no nerve-cells, doubtless one of the reasons why this type of animal does not seem to have led on to any other. But in some sponges, e.g. Pachymatisma, the large exhalant openings can be rapidly closed, e.g. when an inquisitive worm inserts its head. The closure is due to the contraction of a ring or sphincter of spindle-shaped cells, which might be called "neuro-muscular" since they are at once irritable and contractile. In the freshwater Hydra, however, there is the beginning of nervous tissue, and in very simple expression. To the inner aspect of the outer or ectodermic covering cells, which show considerable division of labour, there is a loose network of nerve-cells or ganglion-cells which give off delicate fibres. Some of these are connected with the contractile roots of muscular-cells, and might be called motor. But among the outer covering cells there are also minute sensory cells with ingrowing fibres. Already there is the essence of nervous tissue.

In sea-anemones and some other Cœlentera the division of labour in nervous tissue is more distinctly defined. Superficially there are sensory nerve-cells (S), which receive stimuli and also pass on

the impulse by an afferent fibre to subjacent ganglion-cells or motor nerve-cells (M). Each of these gives off an efferent nerve-fibre to a contractile element. Thus the chain has but two links—sensory and motor nerve-cells—before it comes to the muscular cells, which are often called the "effectors". Neuron is a convenient word for an entire nerve-cell along with its branches or fibres.

From earthworms and their relatives onwards, there is often a third link in the chain. The sensory neuron leads to an associative (communicating or internuncial) neuron which is in turn linked to a motor neuron. This makes a complete neuromuscular arc, as has been already explained in the physiological section. If we use the first letters of the terms, we have S (sensory), A (associative), M (motor), and E (effector or muscular); S, A, M, E making a convenient mnemonic for those who are not familiar with these matters.

To a complete neuromuscular arc there is not in higher animals any *essential* addition. The principle of the linkage is completed in the earthworm's S, A, M, E. But it will be understood that instead of a single sensory neuron at a strategic point, there is usually an integrate of numerous cells making a sensory spot or organ. The fibres from these cells may combine to form a sensory nerve, leading to associative and motor neurons combined to form a ganglion. The efferent fibres from the motor cells of the ganglion combine to form a motor nerve which divides up into its fibres when it reaches a muscle.

On a muscle fibre there are not only the motor-endings of motor fibres, which induce contraction, there are sensory nerve-endings by which messages from the muscle are carried by sensory fibres to sensory neurons.

Ganglion cells are of very varied shape, but each consists of a cell-body giving off branches. The cell-body contains a nucleus and the cytoplasm shows characteristic granules and some evidence of structural intricacy. One of the outgrowing processes of a motor neuron is relatively long, branches very sparingly, and is known as the axis-cylinder. In all but a few of the simplest Metazoa, this nerve fibre is surrounded by a sheath called the neurilemma, said to be formed by adjacent connective tissue; and in Vertebrate animals each nerve fibre has in addition a medullary sheath. But even in the higher Vertebrates there is an interesting persistence of the Invertebrate type of non-medullated or simply contoured fibre. These occur in the sympathetic and olfactory nerves, and also in all the nerves of the lamprey, the hag, and the lancelet, which are primitive Vertebrate types. It is instructive to find this structural detail confirming the derivation of Vertebrates from Invertebrates. Besides the axis cylinder, the ganglion cell usually shows short processes which ramify like the branches of a tree, and are called "dendrites". They touch the dendrites of other neurons.

Nerve fibres arise as outgrowing prolongations of ganglion cells, which extend themselves in the embryo in a manner reminiscent of an Amœba sending out pseudopodia. In a suitable medium the fibres may continue growing for weeks from a fragment of isolated embryonic nervous tissue, and the occurrence of something like amœboid movement at the tip is a good instance of what may be called the conservatism of Organic Evolution.

Nervous tissues always arise from the outer or ectodermic layer of the embryo, as might indeed be expected. For this is the layer in which, in the course of history, it has been most important that protoplasmic irritability should find expression. For the outer surface is, to begin with, the layer most directly amenable to external stimulus. But why some ectodermic cells should form epidermis and scales, while others form sensory patches or sink in

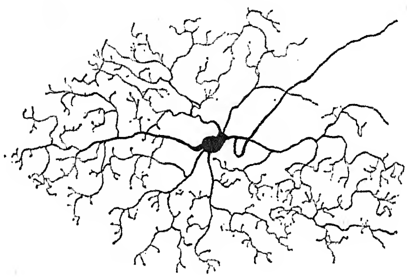


FIG. 103.

Extraordinarily branched nerve-ending of a sensory neuron. After Cajal.

to become ganglia, is one of the unanswered questions of embryology, raising as it does the whole problem of differentiation.

A cross-section of a nerve usually shows several bundles of nerve fibres, each bundle enclosed in a connective tissue sheath (perineurium) with ingrowing partitions. Like electric wires in some non-conducting substance, the bundles are embedded in a matrix of connective tissue; and in this there may be seen an artery, a vein, and a lymphatic vessel. Ensheathing the whole nerve there is an outer sheath of connective tissue, the epineurium.

A nerve fibre itself is soft, cylindrical, glassy, with constrictions or nodes at intervals, and with peripheral nuclei in the internodal regions. In the centre of a main fibre there is the neuraxon or axis cylinder, and between it and the external neurilemma there is, as mentioned, in most Vertebrate nerve fibres a whitish "medulla" of fatty myelin. When the axis cylinder reaches a muscle fibre it spreads out into a branched motor-ending with many nuclei. The neurilemma sheath of the nerve fibre becomes continuous with the

sarcolemma sheath of the muscle fibre. When a motor fibre is followed inwards towards the cell from which it grows out, there is a disappearance of neurilemma, nodes, and medulla.

In the core of a nerve fibre there are indications of fibrils. These are regarded by some as the essential elements in the transmission of impulses, while others maintain that the essential part is the less compact, sometimes wellnigh fluid stuff between the fibrils, or that the fibrils are but the walls of tubes within which the essentially nervous substance lies. These are details awaiting still more penetrating analysis. But the important point in an outline survey like ours is to understand that the principle of the nervous system is simple—consisting of interlinked sensory, associative, and motor neurons, which integrate the whole body.

In outlining the *evolution* of nervous tissue, we may begin with undifferentiated external ectoderm, whose cells are in part contractile and in part sensitive. In sponges there are no distinguishable nerve cells, but in some types, as we have mentioned, there are slowly contractile cells which respond to external stimulus, and may therefore be called neuromuscular.

In Hydra a specialised superficial sensory cell may send a fibre to the adjacent contractile root of a muscle cell; or it may send a fibre to one of the insunk ganglion-cells, whence the stimulus passes to a muscle root.

In sea-anemones and medusæ the stimulation of a tentacle may be followed by movement of part of the body at some distance. This implies superficial sensory cells with fibres passing to a deeper network of ganglion cells; and these may pass on the impulse to muscle cells directly, or to other ganglion cells which affect more distant muscle cells.

Earthworms may be taken to illustrate a further step; for they show a centralised nervous system in the form of a ventral nerve-cord. A sensory neuron in the skin sends a fibre into the nerve-cord, where it divides into an anterior and a posterior branch. One of these branches communicates with those of an associative neuron, whence the impulse is transmitted to a motor neuron, and so by an efferent fibre to the muscles of the body-wall. But in some cases in the earthworm the second link in the chain is omitted, and the impulse passes directly from sensory fibre to motor neuron, as is occasionally true even in Vertebrates. For an indication of further steps we must refer back to the physiological section, but attention must be called to the anatomical fact that in ordinary Vertebrates the cell-bodies of the sensory neurons, except in the case of those concerned with smell, have sunk into the spinal ganglia beside the spinal cord. From these deeply insunk sensory neurons fibres pass into the cord while others extend to nerve-endings on the surface, which are often surrounded by a special group of epidermic cells.

MUSCULAR TISSUE.—An Amœba is a diffusely contractile single cell, without any specialised motor structures, but in many Protozoa, as in the stalk of the Bell Animalcule (Vorticella), there is the beginning of differentiation in the form of threads or myonemes, and the very frequent cilia and flagella are other familiar illustrations. In a cilium the protoplasmic thread is alternately flexed and straightened again; in a flagellum there is an undulatory movement along the length of the thread or lash.

In sponges there is incipient muscular tissue, taking the form of rings or rows of spindle-shaped cells; but most of the contractile activity of the sponge is in the flagella of the internal cells that keep up the inhalant and exhalant currents of the characteristic canal system.

In Hydra and some other simple Cœlentera the bases of some of the epithelial cells of the outer and inner layers (ectoderm and endoderm) are prolonged into contractile roots. This is an interesting division of labour, for the contractility is mainly restricted to the basal processes. A somewhat similar primitiveness is seen in the muscle cells of threadworms (Nematodes), where the inward-projecting portions are as markedly non-contractile as the outer portions are contractile. The line of evolution has been the reduction of the non-contractile portion of the muscle cell, and many interesting gradations can be seen within the groups of Cœlentera and worms. But from the level of certain Cœlentera, e.g. jellyfishes, onwards, there are specialised muscle fibres, a fibre being either a much elongated single cell or a union of several elongated cells in one line.

In sluggish animals, such as tapeworms and tunicates, the muscular elements are smooth and unstriated muscle cells. Each is an elongated spindle with a central nucleus, and with a longitudinal intracellular fibrillation. These unstriped muscle cells often occur in long rows, the component units very closely apposed. Compared with ordinary striped muscle cells, they are less differentiated, and they contract more slowly. In sluggish animals like molluscs there is much unstriped muscle, but those muscles that do something quickly, such as shutting the shell-valves of a scallop, have striped fibres or fibres with unstriped fibrils twisted in a spiral. In the higher backboned animals, such as mammals, the unstriped muscles are practically restricted to (*a*) the wall of the food-canal (effecting the slow peristaltic movements which press the food onwards), (*b*) the wall of the bladder (effecting the slow contractions in urination), and (*c*) the walls of the arteries. It is interesting to note that in the archaic Invertebrate Peripatus, all the muscles of the body are unstriped, save those that work the jaws!

In a striped muscle fibre the greater part of the cell has gone to form a set of parallel longitudinal fibrils, with alternating "clear and dark" transverse striæ, whose details are somewhat compli-

cated. A residue of unmodified cytoplasm is often to be observed on the side of the fibre, and a slight sheath or sarcolemma represents the cell-membrane. In the superficial cytoplasm, as in man, or more deeply, as in the frog, there are several nuclei. On the surface of the fibre there are also the branched endings of motor and sensory nerves. Numerous muscle fibres wrapped up in a sheath of connective tissue or fascia compose a muscle, which in Vertebrate animals is usually attached to pieces of skeleton by means of sinews or tendons of living connective tissue. In Arthropods the highly developed muscles are attached to the skeletal parts by non-living strips of chitin, so that there is a marked structural difference between Vertebrate and Arthropod tendons.

CONNECTIVE TISSUE.—While nervous and muscular tissues are well defined, those included as connective form a heterogeneous group. Their chief functions are to enswathe, to bind, and to support. In some cases, like the fascia that covers a muscle, the component cells are bound together without any intercellular matrix. Not infrequently they become laden with fat, or sometimes with pigment. Very different, however, are those forms of connective tissue in which there is an intercellular matrix, which the cells make, as in gristle or cartilage. Connective cells are often very irregular in shape, giving off fine processes in the matrix, well seen in bone cells. Another modification is seen when the connective cell forms a long fibre, as is well illustrated by tendons. Besides the firm forms of connective tissue, we are logically bound to include fluid tissues—the blood and the lymph; and in Invertebrate animals the cœlomic or perivisceral fluid may be very important, as in the sea-urchin.

GENERAL.—The concept of a tissue implies aggregation of cells, and sometimes integration as well, as in nervous tissue, where the cells work into one another's hands; but we re-emphasise that in most animals with differentiated *fixed* tissues there is a common medium of *fluid* tissue, usually the blood. And besides this fluid tissue there are more or less independent cells, the amœboid wanderers, notably those leucocytes that are able to migrate out of the blood and the larger phagocytes (macrophages) which move about in the tissues. If a tissue be compared to a street of similar houses, there are also some houses that move from one street to another, as we may see them doing in America.

We cannot leave the animal tissues without again referring to the method of tissue culture especially associated with the work of Ross Harrison and Carrel. It has been found possible to keep small fragments of tissue, especially young tissue, alive in isolation in suitable media, and even to induce them to exhibit cell-division and growth. It has been possible to discover certain media which

prompt growth and others that hinder. Two main results stand out: first, that the structural character of a tissue may be much altered by the environmental and nutritional conditions in which it is cultured; but secondly, that the deeper physiological character of the tissue, as shown by its reactions and modes of growth, may remain strikingly persistent.

PLANT TISSUES

Since the cells of plants are surrounded by very definite cell-walls, markedly contrasted with the delicate cell-membranes in most animals, the tissues are sharply defined, as is evident when we even mention wood, bark, pith, and so forth. Yet on the whole the division of labour is less pronounced than in animals above the level of worms; and the absence of distinct muscular and nervous tissues is enough in itself to indicate how wide is the parting of the ways.

Tissues almost always arise by the multiplication and side-by-side apposition of cells. There are a few very unusual cases, such as the feltwork in some Algæ and Fungi, where tissue is produced by an intertwining of long filaments. In the Early Devonian, before there were any Ferns, there was a small race of unique land plants, the Rhyniaceæ, which show the beginning of *vascular tissue*, destined to play, in Pteridophytes and Spermophytes, such an important part in structural and functional advance, being especially differentiated for the transport of water and food-stuffs and for support. Vessels arise by the fusion of a row of cells, and may be illustrated by wood-vessels and sieve-tubes.

Another contrast between plant and animal tissue is that plant cells are very frequently united by bridges of protoplasm which traverse the cell-walls. This is indeed illustrated among animals, but it is not characteristic. It must help in plants to unify the whole body; and the Sensitive Plant and the Sundew afford signal instances of the rapid propagation of a change from cell to cell over a considerable distance. This must compensate in some measure for the absence of nervous elements in the strict sense.

When a cell divides into two, the halves of the new cell-wall may be pulled asunder, leaving an interspace; and the continuation of this process may result in the development of an intercellular cavity, usually containing air and often of importance in the internal aëration of the plant. Or the same result may be reached by the splitting and recession of two adjacent cell-walls. Rather different in origin are the intercellular spaces formed by the disintegration or solution of cells; and these are oftenest used as reservoirs for water or for waste products. It has been maintained that the resin-

canals of most Conifers are the semi-normal results of strain and stress.

Many of the cells in animals retain throughout life their power of dividing. Thus as the outermost layer of the epidermis or "scarf skin" in higher animals is worn away, it is replaced by fresh growth from beneath; to put it technically, the worn-out stratum corneum is always being renovated by contributions from the stratum mucosum. The same kind of replacement is common in other parts of the body; but there are some cells, notably those of the brain, which do not multiply after birth.

In plants there is much multiplication of cells in parts that are still growing, but in contrast to most animal types there is a frequent persistence of embryonic tissue at strategic points. This *meristem*, as it is called, is well illustrated by the growing point of a stem or of a root, and by the cambium-layer which forms a ring between the inner wood and the outer bast in a Dicotyledonous stem. This local persistence of non-differentiated ever-young cells is very characteristic of plants; but there are also many cases of division of cells in relatively differentiated permanent tissue.

When cells remain rich in protoplasm, thin-walled, well expanded in all directions, the term *parenchyma* is used, in contrast to *prosenchyma*, in which the cells are elongated, thick-walled, pointed at the ends, interlocked, and not usually rich in protoplasm. Thus there is a deep contrast between parenchymatous and prosenchymatous tissues.

All that we wish for our purpose here is an outline survey of the chief plant-tissues, and these include:

(1) the skin in the wide sense—the tegumentary tissues;
(2) the fibro-vascular bundles—beginning to be prominent in Ferns and their relatives;
(3) the fundamental tissue system, mostly parenchymatous, e.g. in the substance of leaf and shoot and root.

(1) The most important tegumentary tissue is the epidermis, usually a single layer of colourless cells, often with the outer walls thickened into a cuticle, and bearing a great variety of superficial structures. When these are entirely epidermic they are known as "hairs", like the glandular papillæ on the Chinese Primrose or the stings of nettles; but when sub-epidermal tissues help they are conveniently called "emergences", as in the prickles of the rose and the glandular tentacles of sundews. Often there are glandular specialisations in the epidermis, such as groups of cells (hydathodes), which secrete watery fluid, or nectaries which secrete sugar, or the pitcher-plant's little pockets which secrete digestive juice. A noteworthy feature of epidermic cells is the interlocking of their cell-walls, which probably reduces the risk of lesions under strain.

Very important are the green "guard-cells" which occur in pairs with a minute opening or "stoma" leading into the internal cavities of the green leaf or green stem. They regulate the diffusion of gases and of water-vapour.

(2) *Fibro-vascular Bundles.*—When we break across the leaf-stalk of the Broad-leaved Plantago, so common by the wayside, and pull the two parts asunder, we see substantial longitudinal strands which are continuous with the midrib of the leaf. These are the fibro-vascular bundles which run through the body of all higher plants. While indicated at lower and older levels, they first come to their own in the Vascular Cryptogams, such as ferns. In these, as in Flowering Plants, they consist of two portions, the wood or xylem and the bast or phloem. The wood consists of elongated cells or tracheids, of vessels or tracheæ, and of wood-parenchyma; it has chiefly to do with the transport of soil-water from the roots to the leaves, and also with support. The phloem consists of vessels called sieve-tubes, with perforated transverse partitions (sieve-plates) at frequent intervals, and of cells more or less parenchymatous. There are, of course, great differences in detail in different kinds of bundles, and in their relations to one another in the stem and in other parts of the plant. They end in the fine strands or veins of the leaf. The bundles are developed from strands of persistent embryonic cells (meristem), and some of this ever-youthful tissue may persist in the bundle, continuing to add to the xylem and to the phloem. This is seen in the "open" bundles of Gymnosperms and Dicotyledons, whereas in Monocotyledons and most Pteridophytes the meristem is early exhausted, and the finished bundle is said to be "closed". The phloem has to do with the transport of part of the proteins, but some of these seem to move in the young wood. It is believed by some botanists that the phloem elements also serve to distribute hormones.

(3) The "fundamental tissue" includes all that is enclosed by the tegumentary layer and traversed by the bundles. It is a collective term for such tissues as cortex and pith, mainly parenchymatous. It helps in support, in conducting materials, in storing reserves and waste products, but in the interior of the leaf it reaches its acme of function in being the photosynthetic tissue. Underneath the upper epidermis this "mesophyll" consists of closely packed cells (the palisade-parenchyma), elongated at right angles to the surface and very richly provided with chlorophyll. It is the chief seat of photosynthesis. Below the palisade cells, and extending to the epidermis of the under surface, where most of the stomata usually lie, there is looser tissue (the spongy parenchyma), composed of more irregularly shaped cells, with less chlorophyll, and with numerous intercellular spaces. It has largely to do with facilitating the diffusion of gases and the outgo or transpiration of water-vapour.

THE CELL

THE CELL THEORY.—As we have seen, not a few of the early microscopists made attempts to define the minute elementary parts that build up living creatures; but it was not till 1838 that the idea of the cell as a structural and functional unit was clearly focused in the Cell-Theory or, better, Cell-Doctrine (Zellenlehre) of Schwann and Schleiden. Its three propositions may be recalled. First, there is the *morphological* statement, that all living creatures have a cellular structure, and that all but the simplest, that is to say all that have what may be called a "body", are built up of cells and modifications of cells. Second, the Cell-Theory includes the *physiological* statement, that the activity of a many-celled organism is the sum of the activities of the componentc ells. This idea requires to be safeguarded by the fact of correlation, for the life of the whole cannot be described without recognising that it is more than the life of all its parts, just as the behaviour of a group of men with a common purpose cannot be adequately described merely in terms of the movements of the individuals. Third, the Cell-Theory includes the *embryological* statement, that the individual many-celled organism begins its life, in all ordinary cases, as a fertilised egg-cell, which divides and re-divides to form an embryo. In other words, developing and growing imply cell-division. Cellular structure is a condition of differentiation.

But after the formulation of the Cell-Doctrine, it gradually became evident that the structure of the unit was complex to an unforeseen and extraordinary degree, just as the atom has slowly revealed the complexity of its organisation in modern physics. The main conclusions of Schwann and Schleiden remain true to-day, but the picture of the cell has become much more intricate.

Convenient objects for examination are easily found, as even by tearing a strip of epidermis from a leaf, say conveniently a garden iris or other free-growing monocotyledon, and then other leaves of various kinds. Endless sources of interest can be established from a single country walk, by taking out a few wide-mouthed bottles, and bringing home in each a sample of weed and water and bottom taken from the different pools and ditches on the way, for each will be found a source of varied wonders well worth searchings, and these repeated for weeks and months on end. With such a growing range of aquaria on the window-sill or microscope-table, one has an unending range of observation and of interest, in repeating for oneself the centuries-long record of such discovery. From this knowledge of Protozoa and Protophytes and various Bacteria, of filamentous Algæ and so on, it is easy to go further, as especially by the sea-shore. Thus the egg-cells of sea-urchins or starfishes are

of obvious interest, and with a little silk net one can fish plankton forms in abundance, with strange larvæ and what not. Returning to the garden, its plants will be found to yield many interests: thus the circulation of protoplasm in the stamen hairs of a Tradescantia will never be forgotten, nor the yet more impressive circulation in Chara or Nitella taken from a pond. So a drop of blood from a needle-prick of the finger well rewards attentive study, and next the comparison of this with a similar droplet from the frog. Again see the varied structure of hairs of different animals, the marvellous peristomes of moss capsules on old walls and rocks, the simple structure of moss leaves, and the interesting and useful complexity of the leaf of the peat-moss Sphagnum—and so on indefinitely, as to the varied scales of butterflies and moths' wings, the age-rings of fish-scales, and whatever else attracts us. In short, in ways without number, one can thus at once play and study with the microscope; and thus

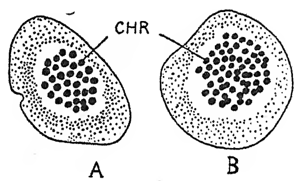


FIG. 104.

Nuclear Chromosomes (CHR) in a Cell. A in the haploid and B in the diploid number.

prepare for its more regular application and use. One is thus beginning anew with the old microscopists, and may rapidly recapitulate their main discoveries, especially when thus aided by any of the various introductory manuals, though it is best to begin even without help of these. Enough at the outset to have a lesson or two on the handling of the microscope and its objects from some more experienced friend. Later on, the late Sir Arthur Shipley's *Hunting with the Microscope* will give the beginner sound advice, at once shrewd and entertaining.

Yet the study of fresh material is often very disappointing, since at first one sees so little; and thus recourse is had to methods of fixing, staining, and clearing which bring out fine details of structure in the cell. There can be no manner of doubt that the methods of fixing and staining technique, of which we have previously given a glimpse, have greatly contributed to the intimate modern knowledge of the microcosm of the cell. Without differential staining we could have known little of the complicated processes of cell-division and fertilisation. No small part of the modern advance in the study of heredity has been due to a more penetrating knowledge of the

cell and of its nuclear chromosomes in particular. The microcosm of a typical cell includes the following structures:

(*a*) There is the general cell-substance or cytoplasm, consisting partly of the genuinely living protoplasm and partly of materials (metaplasm) not really living.

(*b*) Almost invariably there is a kernel or nucleus, also protoplasmic and also a little world in itself.

(*c*) A specialised body, called the central corpuscle or centrosome, lies in the cytoplasm near the nucleus. It divides into two before cell-division occurs, and seems to play an important part in the process.

(*d*) In the cytoplasm there may be formed bodies more or less permanent, which are quite different from temporary stores of

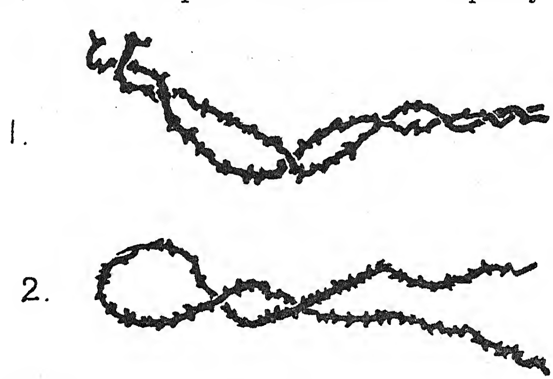


FIG. 105.

Two Living Chromosomes showing their paired state and irregular outline. After McClung.

reserve material and the like. Thus there are often scattered "*mitochondria*", thread-like or rod-like in appearance, which have a rôle in the characteristic activity of the cell, e.g. whether nervous or glandular. They are often visible in living cells. Then there is the knot-like "*Golgi apparatus*", probably part of the genuine protoplasm, and very generally present though difficult to demonstrate. Third, there are "*chromidia*", consisting of immigrant fragments or extensions of the nucleus.

(*e*) Enclosing the whole is a semi-permeable cell-membrane, usually very delicate in animals, strengthened in plants into a very definite cell-wall of cellulose.

THE NUCLEUS.—The centre of the cell, the nucleus, was discovered more than a century ago by Robert Brown. It is a much studied world, and the details presented by fixed and stained specimens seem to correspond somewhat closely to reality. In a normal resting nucleus there is a fine skein of a material called "linin", and

on this there lie scattered granules of a protein substance which stains deeply and is therefore called chromatin. The nucleus also contains a compact body called a nucleolus. Such is the resting nucleus, but in the process of cell-division (the mode known as "karyokinesis" or "mitosis") the appearance becomes very different. The skein or network disappears, and the chromatin becomes concentrated into sharply defined bodies called chromosomes, definite in number for each species. The lowest number is two, seen in the cells of *Ascaris megalocephala*, a common Nematode parasite of the horse. One of the largest numbers is 64 in the horse itself. Man's number is 48. Just outside the nucleus, and probably arising from it,

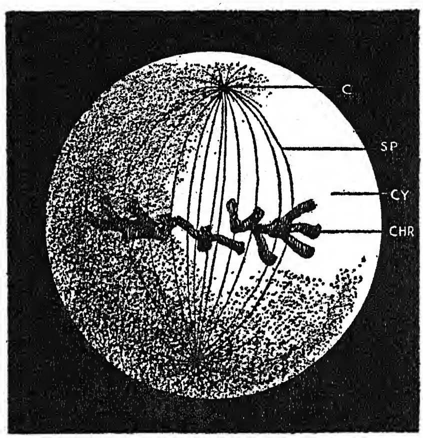


FIG. 106.

Stereoscopic View of a Dividing Cell. C, the centrosome, surrounded by an astrosphere of radiating threads; CHR, the chromosomes on the equatorial plane; SP, the central spindle of threads running from pole to pole; CY, the general cytoplasm of the cell. From a model.

is the small body called the centrosome. This divides into two, and the two halves move to opposite poles of the nucleus and become the centres of what appear in the fixed cytoplasm as very delicate rays. At the equator of the nucleus the chromosomes arrange themselves in a horizontal plane, at right angles to the long axis of the cell, or to the line between the two centrosomes. Each chromosome is then split up the middle longitudinally, as one might split a wooden match into two. The limits between the nucleus and the cytoplasm outside become vague, and the spherical appearance of the nucleus is replaced by a more or less biconical spindle shape. Then a remarkable thing happens: one half of each longitudinally split chromosome moves towards each centrosome—pushed or pulled, who shall say? In any case, the half-chromosomes move along the delicate fibres which run from centrosome to centrosome (so forming the "central

spindle") or from centrosome to equator (the "equatorial spindle"). In this arrangement there is a curious likeness to that of iron filings round a magnet or arranging themselves on a plate under electrical influence. Then the cell constricts and separates the two poles from one another, thus soon forming two daughter-cells, each with its normal number of chromosomes, and each with a centrosome. The chromosomes gradually sink back into the resting network state, and there is a restoration of the apparently simple *status quo* after a complex and meticulously precise process of division.

TYPES OF CELLS.—Many of the Protozoa are so highly organised that it seems clearer to speak of them as non-cellular rather than as single cells; but the Amœba at least is so simple that it may fairly be regarded as the most generalised type of cell, displaying within itself all the great functional properties, e.g. of contractility, irritability, secretion, growth, reproduction.

Casually examined, the Amœba is a blob of viscid protoplasm of irregular and changing shape, containing numerous dark granules, clear spaces or vacuoles, and a central body of more definite shape and solid appearance, the nucleus. Very similar in appearance are the leucocytes or white blood-cells of the Vertebrates; indeed these are hardly less independent or less complete in themselves than the Amœba. But specialisation is the dominant note in the cells of the Metazoa (just as specialisation for particular conditions of life is seen in the more highly organised cell (or cell-equivalent) of the Protozoa) and these specialisations of cells deserve to be illustrated.

In the blood of mammals the Amœba-like white cells are far outnumbered by the red blood corpuscles, small disc-like cells whose chief function—that of carrying oxygen combined with the pigment with which they are highly charged—quite dominates over the other activities of the cell, so that there is not even a nucleus; there may be five million of these cells in a cubic millimetre of blood. Less specialised are the cells of epithelial tissues, which are found as coverings in the body, in part externally, but also lining the alimentary canal, the air passages, the blood-vessels, and so on. Their chief adaptation is that of presenting at the surface a compact pavement, which may, in certain cases, be ciliated. Or again, the cells may be glandular, with the power of forming special substances (such as digestive juices) which they pour out into the cavity they surround. Much more specialised are the nerve-cells. These have a central portion of very variable size and shape surrounding the large nucleus, and a series of fine processes, often also several short branching connections to neighbouring cells, and finally a single nerve-fibre of very great length, along which the efferent or outgoing nervous impulse travels. Then there are the cells of smooth or unstriped muscle, which are elongated spindles—with an oval central

part around the nucleus, and extending from this in opposite directions the fibre-like portions with the power of contraction. Striped or skeletal muscle, again, is still more highly specialised; the fibres may be over an inch long and angular in section; close to the surface may be seen the nuclei, of which there may be even many hundreds in a single fibre, though each fibre behaves as a single cell. In the connective tissues, which include bone, cartilage, and fat, there is usually a light scaffolding of straggling cells and a non-living ground substance of very variable nature, according to the particular kind of tissue.

TAXONOMIC

THE PROBLEM OF SPECIES

Not only herbalists and zoologists, but ordinary observers, to this day, recognise plants and animals "according to their kinds"; witness oak and mistletoe, rook and robin, each of which there is no mistaking; and also other plants and animals without number, as observation goes on; hence, it seems that, like Adam of old, we can name all manner of creatures. Yet as we come to know more and more of them, and look at them more closely, trouble begins. Are our big oak-trees all of one kind? So it at first seemed, even to woodman and carpenter; yet the simple villager, seeking the best acorn-forage for his swine in autumn, may well have noticed that some trees bear their acorns on stalks, while others have them seated close on the branch. If so, he thus anticipated *Quercus robur*, var. *pedunculata* and var. *sessiliflora* of Linnæus, who, as our modern Adam, in such ways advanced the naming of species, and varieties, to a new clearness; and with acceptance accordingly in the main, and almost without question, until the coming in of evolution doctrines. Indeed, practically to this day; for though we no longer accept his conception of species, as in direct descent from those originally created, we still in our way hold that descent doctrine, though now extended from variety to species, to genus, and to larger and larger groups again. Indeed, in a way, we conserve his conception of varieties too, though now so vastly stretching it out; since all the species of a great genus and more have for us arisen as varieties of some far-back species; all more or less preserving their fundamental likeness, yet increasingly accenting and accumulating their variations too, until these may even be so great as to conceal their likeness not a little. Indeed, Linnæus, for all his strictness, was coming to a pretty clear notion of this, in fact was on the way to becoming an evolutionist; for he at length saw that many of his "distinct species" of a large genus

might originally have been but varieties of a few central ones; and indeed these have been increasingly used to mark, and group, "sub-genera" accordingly. Then, too, with increasing knowledge and larger collections, forms appear with intermediate characters between what at first seemed distinct and easily described species; and this happens in some cases so freely that willows, roses, brambles, hawkweeds, etc., have remained perplexing to systematists from Linné's times and earlier ones to our own, though now fresh light is forthcoming.

Systematists, however, throughout their work, still have in the main no choice but to keep by the distinct forms they can observe, describe, and identify, and not speculate about ancestries they do not know: so here it is worth recalling that Darwin left a legacy towards continuing the *Index Kewensis*, the Kew Gardens list of their new plants, thus substantially continuing Linné's herbarium descriptions. We are thus ready to utilise both conceptions of species; for practical purposes still that of characteristic form, and generally with much the same habitat and way of life as well; and secondly that of common ancestry, as we can make this out—a task probably often now impossible, always extremely difficult, and at best only beginning. Thus Johannsen, one of the foremost plant-breeders, who first produced "pure lines", calls the taxonomist's formal and apparent species *phenotypic* species, and the true genetic ones which he and others now seek to identify, *genotypic* accordingly. That most enthusiastic of geneticists, Lotsy, goes so far as to describe the former as little better than special creations of Linné, and thus as "Linnéonts"; while the still more precisely described varieties of Jordan (up to about 200 in the common little cruciferous weed, *Draba verna*, albeit a single species to ordinary eyes as distinct as any) he similarly honours, and derides, as "Jordanonts"! For other species than verified genotypes, he has thus little use; yet we must go on as we do until we get them. Indeed, we take it that the most of Linné's species, and maybe most of Jordan's varieties too, will be justified anew; though cleared of mere hybrids and of forms of different breeds and races merely convergent, through adaptation to similar conditions. In this direction the Mendelian breeders are now making remarkable advances; but more especially in detail, and thus as yet doubtfully helpful in illuminating the origin of species, let alone of larger variations upon the genealogical tree. Here great hopes have been aroused by De Vries's *Mutations*, for him clearly important enough to rank as new species, and even to throw light on their distinctiveness, as veritably "explosive" changes into new forms, persistent until a fresh mutation may occur. He thus throws aside, as practically of no evolutionary value, all those minute variations on which Darwin and his successors, even to Weismann included, have so much depended,

towards gradual formation of distinct species; and he practically restricts the evolutionary importance of natural selection to that of mutations alone. The cause of such large variations remains unexplained; as for the smaller ones mainly relied on by Darwin, they remain "spontaneous and indefinite" accordingly, pending interpretation.

De Vries assumes—as seems for any theory reasonable—that variations and mutations alike could and should take place more readily and more frequently in the geologic past; and these the more the further back we go, since the continuity of heredity had then far fewer generations to evolve, in fact to steady itself in. So thus—as early and large mutations—he interprets all the fundamental characters of great groups, even to the "big lifts", and consequent big gaps in continuity, which we have so long been seeking to fill by intermediate forms or missing links; and, despite some fortunate finds, as yet so incompletely.

Unfortunately for this Mutation theory, however, its main experimental basis—that of the mutations of an American evening primrose (*Œnothera Lamarckiana*) described by him as new species—has been adversely criticised by other and yet more scrupulously careful breeders, who consider these new forms as but reappearances of ancestral characters from what they regard as an uncertainly variable stock, and even more or less complicatedly hybrid as well. So even De Vries himself has since seemed shaken in his convictions. Still, his arguments do not rest on this alone.

His work has been widely stimulating, and must remain of historic interest as a step and link in progress. For while retaining from Darwin the potent agency of natural selection, and not only reviving, but concentrating on, "sports", to which Darwin naturally gave some importance, De Vries has also been a pioneer of exact genetics. And this not only as one of the three re-discoverers of Mendel's principles in 1900, and helpfully suggestive to later Mendelians, but also, by his "pangene" hypothesis towards interpretation of inheritance in its details, to that minute interpretation of the arrangement of genes within the chromosomes of the ovum which T. H. Morgan and so many others have been labouring to decipher. Among the supporters of De Vries's general doctrine of mutation, with independent evidence from other plant-types, may be noted Blaringhem, whose *Transformations brusques des Etres vivants* (Flammarion, 1920) still affords a useful survey of this line of investigation.

Definitions of Species.—Here we may include a few samples of the many definitions of species that have been proposed:

"The Species is an ideal *entity* as much as the genus, the family, the order, the class, or the type (all these equally ideal (or real) in nature).

"But *individuals* truly exist in a different way; no one of them exhibits at one time all the characteristics of the species. . . .

"As representatives of Species, individual animals bear the closest relations to one another; they exhibit definite relations also to the surrounding elements, and their existence is limited within a definite period."—AGASSIZ, 1859.

"Species are merely those strongly marked races or local forms, which when in contact do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin and to be incapable of producing a fertile hybrid offspring."—WALLACE.

"Separate origin and distinction of race, evinced by a constant transmission of some characteristic peculiarity of organisation, constitutes a species."—PRITCHARD quoted by WALLACE.

"An assemblage of individuals which resemble each other in their essential characters, are able directly or indirectly to produce fertile individuals, and which do not (as far as human observation goes) give rise to individuals which vary from the general type through more than certain definite limits."

"No two living beings are exactly alike, but it is a matter of observation that among the endless diversities of living things, some constantly resemble one another so closely that it is impossible to draw any line of demarcation between them, while they differ only in such characters as are associated with sex. Such as thus closely resemble one another constitute a *Morphological species*."—HUXLEY, 1877.

But let us now consider this difficult question in more practical mood.

WHAT IS A SPECIES?—Most people know the stoat and the weasel and could never confuse the one with the other; and these are two nearly related species, which are often distinguished in technical language as *Mustela erminea* and *M. nivalis* respectively. They are two species of the genus Mustela, and one does not require to be an expert observer to recognise that they are nearer to one another than to an otter in the genus Lutra, or to a badger in the genus Meles. Thus it is evident that a species is a group of similar individuals that have a good many characteristics in common, yet are clearly distinguishable from other groups of similar individuals.

In the same way it is not difficult to distinguish the large raven from the much smaller carrion crow, and both of them from the rook, with its rough, bare patch round the base of the bill. Given full-grown specimens, no one has any difficulty in distinguishing these three species of the genus Corvus, the raven (*Corvus corax*), the carrion crow (*C. corone*), and the rook (*C. frugilegus*). But a little cloud of difficulty begins to form in the sky when we turn to

the hooded or grey crow (*C. cornix*), for while the ash-grey of part of the plumage is very distinctive, we know that the bird interbreeds freely with the carrion crow, and that the hybrids are fertile. So ornithologists ask one another whether the hooded crow is really a true species by itself or only a race within the carrion crow species.

In many cases there is no practical difficulty in regard to the limits of a species. Thus in the Northern Hemisphere there is only one species of solan goose or gannet, *Sula bassana*; and although its plumage changes considerably in the course of its life, no one proposes to establish sub-species. Similarly, there is in Britain only one species of kingfisher. But with many other "kenspeckle" birds, the difficulty arises that the species often includes sub-species, as in the case of starling, song-thrush, and golden eagle (to take three diverse instances); or that a country has several related species of the same genus, which are not always very easily distinguished, as might be illustrated by gulls, crossbills, and sandpipers. Since evolution is going on, there is nothing surprising in the occurrence of variations within a species, but what we are now referring to is the frequent occurrence of sub-species or races which breed true and form recognisable smaller groups within the species. There is nothing clear-cut which enables a naturalist to say that such and such distinctions warrant a separate *species* name, while others do not warrant more than a separate *race* or *variety* name.

Yet there are several common-sense criteria of a "good species", which work out well when taken together as far as opportunities permit. First of all, the species characters should exhibit a considerable degree of constancy from generation to generation. Thus very variable characters, like colour and markings, are not to be relied on confidently. It is difficult to get two ruffs or two buzzards which are anything like identical; and yet there is the counter-fact that in other cases a minute feature may be quite decisive. It is sometimes possible to distinguish one species of fish from another by a few scales, or one species of bird from another by a few feathers. A fox can be distinguished from a wolf by its blood-crystals.

The classifier is always pleased when he discovers some particular feature that can be relied on as a test, but, apart from these reliable clues, he knows that the characters on which he takes it upon himself to give a group of similar animals a new species-name must be bigger than those which distinguish the members of a family, using the word here to mean the progeny of a pair. It would never do to emphasise as a species-character some little detail of plumage, e.g. in the Red Grouse, for this might lead to the absurdity of putting two members of one family into different species. Absurd, we say, yet it has repeatedly happened in a study of newly discovered animals that the male has been made the basis of one new species, and the female of another! The cautious classifier would

like, of course, to examine both sexes of his new species, and a series showing juvenile, adolescent, mature, and senescent phases, but it is often very difficult to fulfil these requirements, e.g. when one is describing a collection of novelties from the Deep Sea.

A third consideration, but also difficult to apply, has to do with fertility and sterility. When two related species have been defined in a manner quite satisfactory to the sceptical inquirer it should be possible to say that they do not readily cross and yield fertile offspring. Apple and pear are two species not very far apart, but the pollen of the one is useless for the other. Rabbits and hares, which are much more distantly related, never have hybrid offspring. It is doubtful if they ever try to cross. And although there are some exceptions, such as wolves and jackals, mallard and pintail, it is an important criterion that while members of a species are usually fertile *inter se*, they are rarely fertile with other species. But the difficulty is to apply the criterion. Moreover, there are some cases where varieties or races that are usually referred to the same species will not have anything to do with one another as mates. Such facts point to the reasonable conclusion that while a species is a group of similar individuals with a certain individuality, sometimes structural, sometimes biochemical, sometimes habitudinal, these individualities of species are very unequal when compared with one another.

The fourth consideration which should be kept in mind is plasticity or modifiability. Many types of living creatures are constitutionally obstinate, or so well poised, in their activities and in their architecture alike, that they are not much influenced by changes in nurture—that is to say, in environment, food, and habits. But other creatures are individually very plastic, plants more than animals, sedentary animals more than active ones. It is therefore important to ask whether some species-characters and race-characters may not be the results of similar environmental, nutritional, and habitudinal dints, which are hammered afresh on to each successive generation. Two nearly related species may be inherently much less different than they seem, for each, with its own peculiarities of nurture, may be bearing the imprint of individually acquired modifications. If this be so, the fourth criterion of a good species must be experimental. Are the species-characters altogether innate, or are some of them similarly impressed on the successive crops of individuals who live in particular niches of environmental and nutritional opportunity? The application of this test of species is extraordinarily difficult. It is a relief to come back to Plato and recognise in each species a distinct idea. But the ideas change in space-time, and we have still to ask: *What is a species?*

THE MAKING OF A SPECIES.—A species, as we have explained, is a group of similar true-breeding individuals which are themselves

and no others, and which keep themselves to themselves, not readily breeding with other species! Thus the raven, the carrion crow, the rook, and the jackdaw are all species of the genus Corvus. If a particular species, such as a weasel (*Mustela nivalis*) is satisfactorily defined, and is really worthy of having a second name (*nivalis*) all to itself, then (1) it should show a certain constancy in its distinctive features, breeding true from generation to generation; (2) its distinguishing features should be greater than those which occur in a family circle, i.e. the offspring of a pair; (3) its members should always be fertile with one another, and not readily with those of a related species; and (4) the species-characteristics should be demonstrably intrinsic and not due to the modifying influences that similar surroundings, food, or habits exert on successive crops of individuals. These, as we have just explained, are the four criteria of what may be called a "good species".

But within a species it is often possible to distinguish minor groups of similar individuals also breeding true, and these are called sub-species or races or varieties; and it is often convenient to mark them by a third name tacked on to the second name of the species. Thus we call the Mountain Hares of the Scottish Highlands by the name *Lepus timidus scoticus* and the Mountain Hares of the Alps, *L. timidus varronis*. That is to say, they are two sub-species of the Scandinavian species *L. timidus*; and though some naturalists laugh at these three-barrelled names, there is much to be said for them. Thus, in the case noted, they indicate right away that the Mountain Hares or Blue Hares of the Cairngorms on the one hand and of the Alps on the other, are much nearer to one another than they are to the Brown Hare, *L. europæus*, or to the Irish Hare, *L. hibernicus*. This kind of question is not verbal at all; it is a matter of clear thinking and clear seeing; and it has been admirably discussed afresh by Mr. G. C. Robson in his book, *The Species Problem*—a fine example of clear-headed scientific scholarship and patient inquiry. But what we wish to discuss now is not the definition of a species, but how species arise—and we must not forget that they are arising even in our midst to-day. Here we are, deliberately, in part anticipating the evolutionary discussion of a later chapter.

An understanding and acceptance of the evolution idea must have been hindered by the frequent use of the French word *transformisme*. which suggests the erroneous idea that one species turns into another. To this day we hear ill-informed anti-evolutionists demanding to be shown a case of one species turning into another. But that is not what happens; it would be magic! What does happen is that novelties or variations arise within a species, diverging on a path of their own—a path which may lead to destruction, or, in other cases, to the establishment of a new sub-species or variety or race, and by and by, perhaps, a new species, that is to say, a

group so distinctive that it deserves a name all to itself. Most ornithologists believe that the Red Grouse, a bird peculiar to Britain (apart from introductions elsewhere), is derived from the Willow Grouse, at home in Scandinavia, but no one believes that a Willow Grouse turned into a Red Grouse.

The first step in the origin of a new species is the emergence of variations or mutations, whose causes are still very obscure. That is a separate problem—the origin of variations or mutations, presumably from some shuffling of the hereditary cards or from some deep change in the constitution of the germinal protoplasm. These variations are very common, and it is not for our present purpose begging any question to take them as given.

A second step in the evolution of a new species is the inbreeding of similar variants. If the same new departure has been exhibited about the same time by a number of individuals, these may interbreed, and this will tend to increase the ranks of the contingent bearing the new features. If a variant does not find a similar variant with which it can breed, it may pair with a member of the original stock; and if the novel character is a Mendelian "dominant" to its absence or its counterpart, the offspring will all resemble the variant in that respect; and in the next (second filial) generation the number of individuals bearing the novel feature or features will have considerably increased. The more the similar variants interbreed, the more fixed and widespread will the new feature become. Thus there is the beginning of a new race or variety. In this way some strong breeds of domesticated animals and races of cultivated plants have arisen from a few original variants or even from one.

Another factor in the making of a species is isolation, a general term for the various ways in which the range of inter-crossing is lessened. One of the simplest of these ways is literal insulation, for when a new departure occurs on an island, or on a peninsula that becomes an island, there will be more likelihood of similar forms pairing together. Some Field Mice (*Apodemus sylvaticus*), the commonest mammals in Europe, seem to have been carried as stowaways on a fishing smack from Scotland to the Fair Isle off Shetland. They flourished and multiplied there and a new departure arose, which was helped by its insulation to become a successful race, and by and by a new species, *A. fridariensis*. This is, in any case, a reasonable interpretation of what occurred. Of recent years some of the Fair Isle Field Mice seem to have been introduced into the Island of Foula, about sixteen miles out in the Atlantic to the west of Shetland; and there the story has repeated itself. For now a new sub-species, *A. fridariensis thuleo*, has been established. But relative isolation may occur in other ways, e.g. by a change in the course of a river, by alterations in land level, by differences in the time of breeding, by divergences in habit, by the discovery of

different niches of opportunity, and even by more or less psychological antipathies, such as hares have for rabbits, and some amorous pigeons for other races.

What is most difficult to understand in the origin of a new species is the fact that along with the new features of structure and of habit there is usually associated some degree of sterility with the original stock and with other species. This may be in part correlated with a biochemical incompatibility, and also with a change in the number of the chromosomes which makes cross-breeding impossible or difficult.

Finally, there is the factor on which Darwin laid most emphasis, that the new departure will succeed in establishing itself in direct proportion to the survival value of its peculiar features. The incipient variety may find itself in a slightly different environment, to which it is better suited than was the original stock. Thus it may evolve alongside of the old species, though in many cases, no doubt, it becomes a successful supplanter.